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NEW TAXA AND NOMENCLATURAL CHANGES IN THE GENUS TRICHIPTERIS (CYATHEACEAE)

DAVID S. BARRINGTON

The genus *Trichipteris* was substantially enlarged and redefined by Tryon (1970). However, a number of nomenclatural problems were left unresolved pending a thorough revision of the group. The additions and changes that make up this contribution are the result of my revisionary study of the genus (Barrington, 1974). One new species, two new varieties, new combinations, changes in status, and comments on correct authorship are the result.

Dr. Rolla M. Tryon of the Gray Herbarium, Harvard University, contributed a number of comments and suggestions to this work, for which I am grateful. Dr. David B. Lellinger, of the U. S. National Herbarium, brought to my attention the unusual specimens of *Trichipteris nigripes,* and suggested the epithet "brunnescens." Ms. Mary Robbins provided the drawings of the new species of *Trichipteris* from Guyana (British Guiana).

Trichipteris costaricensis (Kuhn) Barr., comb. nov. *Hemitelia costaricensis* Kuhn, Linnaea 36:159. 1869.

Trichipteris demissa (Morton) Tryon var. **thysanolepis** Barr., var. nov. Plate 1: figures 1 & 2.

Differt a varietate typica squamis petioli fimbriatis, lamina 1-pinnato-pinnatifida, ramis laminare furfure squamularum et trichomatibus longis, paraphysibus longitudine sporangia plus minusve aequantibus.

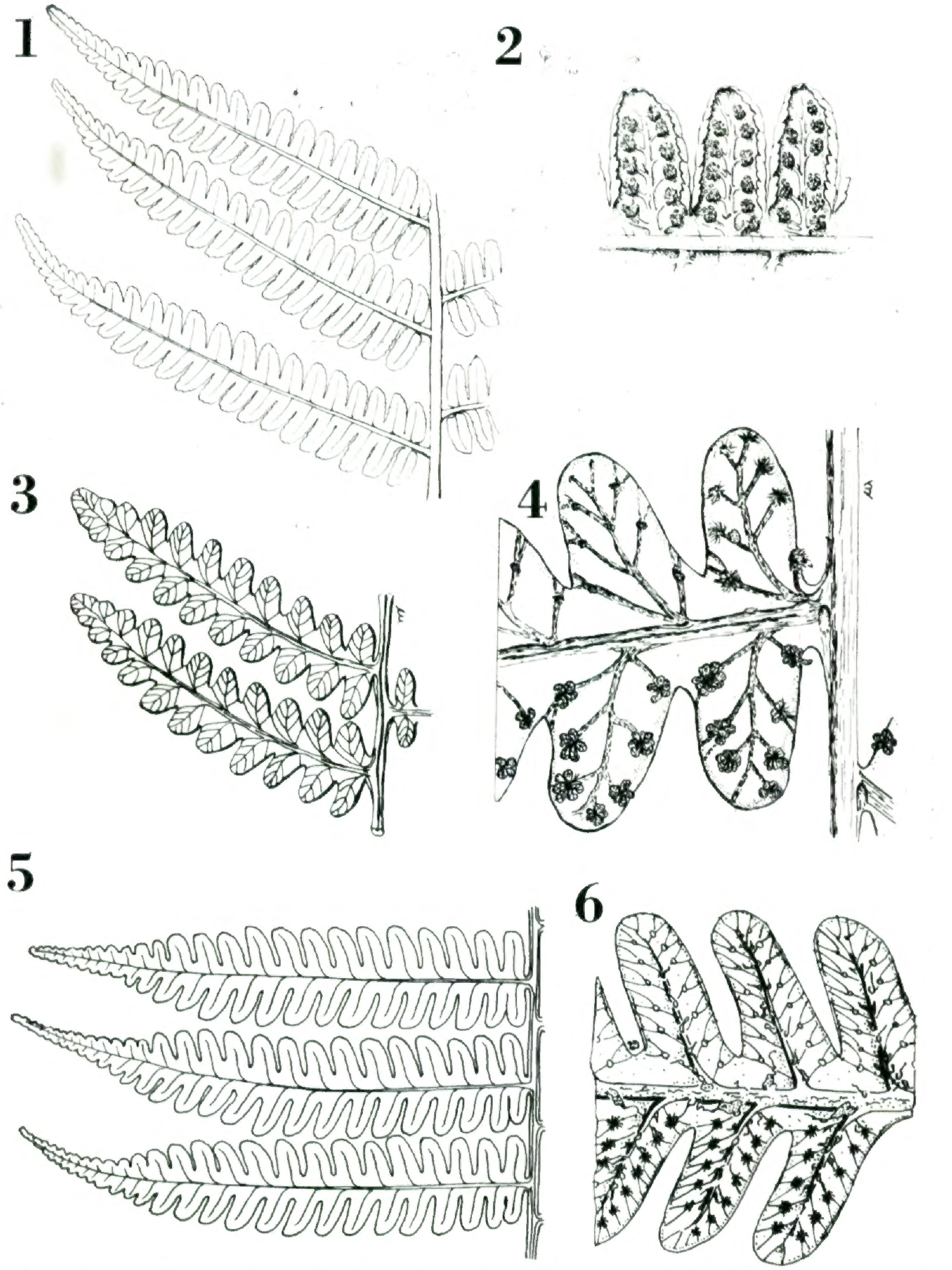

Plate 1. Figures 1 & 2: *Trichipteris demissa* (Morton) Tryon var. *thysanolepis* Barr., var. nov. *Maguire Wurdack & Bunting* 37291, GH; figure 1, three central pinnae × ½; figure 2, three lobes of a pinna × 1½. Figures 3 & 4; *Trichipteris nanna* Barr., sp. nov. *Tillet Tillet & Boyan* 45119, US; figure 3, two central pinnae × ½; figure 4, basal part of a pinna × 2. Figures 5 & 6: *Trichipteris nigripes* (C. Chr.) Barr. var. *brunnescens* Barr., var. nov. *Cuatrecasas* 16155-C, US; figure 5, three central pinnules from a central pinna × ½; figure 6, central part of a pinnule × 2.

Holotypus: Venezuela, Territorio de Amazonas, Summit, Cerro de la Neblina, Río Yatua, January 15, 1954; *Maguire, Wurdack & Bunting* 37291, NY. Isotypi: GH, US. Paratypi: Venezuela, Territorio de Amazonas, Cerro de la Neblina, Río Yatua; *Maguire, Wurdack & Maguire* 42346, US; *Maguire, Wurdack & Bunting* 37100, US.

The varietal epithet, derived from θύσανος (fringe), and λεπίς (scale) refers to the distinctive multicellular trichomes borne along the edge of the petiole scales, which are absent in plants of var. *demissa*. The lamina of var. *thysanolepis* is 1-pinnate pinnatifid, while in var. *demissa* it is 2-pinnate or more complex. The paraphyses of variety *thysanolepis* are longer than those of the type variety.

Trichipteris Dombeyi (Desv.) Barr., comb. nov. *Alsophila Dombeyi* Desv., Mém. Soc. Linn. Paris **6**:320. 1827.

Trichipteris falcata (Kuhn) Barr., comb. nov. *Alsophila falcata* Kuhn, Linnaea **36**:155. 1869.

Trichipteris gibbosa (Kl.) Barr., comb. nov. *Alsophila gibbosa* Kl., Linnaea **18**:542. 1844.

Trichipteris nanna Barr., sp. nov. Plate 1: figures 3 & 4.

Caulis erectus, sed gracilis, ad 1 m. altus, diametro 1.5 cm., inter cicatrices anthracina. Petiolus circa 10-15 cm. longus, ferrugineus, sulcatus, inermis vel pauce tuberculatus; squamis structura late-marginatis fuscis albidolimbatis integris vel erosis, parte media fusca saepe deficienti vel indistincta. Lamina 40 cm. longa, 1-pinnato-pinnatifida obovato-lanceolata coriacea, apicem versus gradatim acuminata. Rhachis adaxialiter sulcata glabra, abaxialiter squamis argentis adpressis. Pinnae centrales sessiles oblonga, base truncata vel cuneata, apice obtusa integra. Rhachides pinnarum adaxialiter sulcatae, glabrae, abaxialiter glabrae vel trichomidiis albescentibus, basaliter pneumotodiis lacriformibus. Costae adaxialiter glabrae, abaxialiter glabare vel trichomidiis albescentibus. Lobi pinnarum integri, apicibus rotundatis, in sicco abaxialiter revoluti. Venae liberae, ad soros submarginales furcatae

vel simplices. Pagina laminae utrinque glabra, vel pagina abaxialis trichomidiis paucis. Sori exindusiati, paraphysibus porphyreis tranlucentibus sporangia plus minusve aequantbus; receptacula hirsuta.

Holotypus: British Guiana, Upper Mazaruni River Basin, Mt. Ayanganna, on shoulder of E. flank, about Thompson Camp; 1418 m., 12 August 1960; *Tillet, Tillet & Boyan* 45119, US.

The species epithet refers to the diminutive size of the plant, relative to that of most tree ferns. From the other 14 small species in the genus, *T. nanna* is best separated on the basis of its blunt-tipped pinnae and blunt, entire ultimate segments.

Trichipteris nigripes (C. Chr.) Barr., comb. nov. *Alsophila nigripes* C. Chr. Ind. Fil:45. 1905. nom. nov. for *Alsophila melanopus* Hook., Syn. Fil. ed. 1:37. 1866. non *A. melanopus* Hassk., Journ. Bot. 7:325. 1855.

Trichipteris nigripes (C. Chr.) Barr. var. **brunnescens** Barr., var. nov. Plate 1: figures 5 & 6.

Differt a varietate typica petiolis aculeatis, ramis laminarum trichomatibus, pinnulis sessilibus vel brevi-petiolulatis.

Holotypus: Colombia, Valle de Cauca, Río Yurumanguí, Veneral, 5-50 m., 1944; *Cuatrecasas* 16155-C, US. Isotypus: GH. Paratypus: Colombia, Valle de Cauca, Agua Clara, highway from Buenaventura to Cali, 100 m., 1944; *Killip & Cuatrecasas* 38884, F. Isoparatypi: GH, US.

This is a Pacific coastal variety of *T. nigripes* which centers in the Dagua Valley of Colombia, an important center for endemism in the genus. It differs from the typical plants of the species in having well-developed petiole spines, sessile pinnules, and trichomes on the leaf axes.

Trichipteris pauciflora (Kuhn) Tryon. *Alsophila pauciflora* Kuhn, Linnaea 36:156. 1869.

The basionym for the combination in *Trichipteris* was cited as "Alsophila pauciflora Presl, Gefässbündel Stipes der Farrn:35. 1847 (preprint from Abh. Bohm. Ges. 5(5): 343. 1848"). However, Presl's name is a *nomen nudum,* and the author of the basionym and reference require correction. For a detailed discussion of this nomenclatural problem, see Nicolson (1975).

Trichipteris phalerata (Mart.) Barr., comb. nov. *Cyathea phalerata* Mart., Denkschr. Bot. Ges. Regensb. **2**:146 *t. 2 f. 3*. 1822.

Trichipteris phalerata (Mart.) Barr. var. **Iheringii** (Rosenst.) Barr., comb. & stat. nov. *Alsophila Iheringii* Rosenst., Hedwigia **56**:358. 1915.

Trichipteris Schlimii (Kuhn) Barr., comb. nov. *Alsophila Schlimii* Kuhn, Linnaea **36**:157. 1869.

REFERENCES CITED

BARRINGTON, D. S. 1974. A revision of the genus *Trichipteris* (Cyatheaceae). Ph.D. Thesis, Harvard University.

NICOLSON, D. H. 1975. Isonyms & pseudo-isonyms: identical combinations with the same type. Taxon **24**: 461-466.

TRYON, R. M. 1970. The classification of the *Cyatheaceae*. Contr. Gray Herb. **200**: 3-53.

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THE OCCURRENCE OF BISPORANGIATE STROBILI IN SUBALPINE BLACK SPRUCE

W. H. WEIDLICH[1] AND J. A. TEERI[2]

Successful growth and sexual reproduction in subalpine black spruce (*Picea mariana* (Mill.) BSP.) in New Hampshire are limited by exposure and the low mean temperature of the warmest month of the growing season, as in the northern parts of the species range (Teeri, 1968). At timberline the frequency of individuals successfully reproducing by seed is much less than in the forests at lower elevations. In Krummholz patches above the timberline, which in the White Mountains of New Hampshire occurs between 4500-4700 ft., reproduction appears to be accomplished primarily by vegetative layering of the prostrate stems, with only sporadic occurrence of female strobili (Teeri, 1969). At the upper elevational limit of female strobilus production (ca. 4,800 feet above sea level), bisporangiate strobili occasionally occur on prostrate plants of black spruce.

Bisporangiate strobili have been reported for many genera of conifers (Chamberlain, 1935) including spruce (Santamour, 1959), and information on the morphological distribution of sexes is present in the literature (Chamberlain, 1935; Richter, 1932; Zobel, 1952; Santamour, 1959; Black, 1961; and Elis, 1970). This paper describes the anatomy of bisporangiate strobili of subalpine black spruce and correlates their occurrence with changing environmental conditions along an elevational gradient on Mt. Washington, New Hampshire.

METHODS

The study area was on an east-facing slope of Mt. Washington, New Hampshire. It included at its lower elevation (2,800 ft.) a well-developed red spruce (*Picea rubens*)-

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balsam fir (*Abies balsamea*) forest. Occasional black spruce colonies were present in this forest in sites subjected to cold air drainage or on wind exposed ridge crests. At the upper elevation (5,000 ft.) the study area was within the alpine zone in which prostrate Krummholz colonies of black spruce were scattered on the tundra. Maximum-minimum recording thermometers were placed in ventilated wood shelters at two elevations in the study area and were read weekly for the 1967 growing season. The shelters were located in the foliage of black spruce plants at each station. Additional temperature data were obtained from records of the weather observatory at the summit of the mountain.

Bisporangiate strobili of *Picea mariana* were fixed in FAA in the field. The fixed strobili were dehydrated in tertiary butyl alcohol, embedded in Paraplast, and sectioned at 10-12 μ on a rotary microtome. The sections were stained with safranin and fast green.

RESULTS

The mean weekly temperatures for the three stations of the transect are illustrated in Figure 1. The right-hand axis indicates the sexual reproductive status of black spruce along the transect. At lower and middle elevations (2,800-4,600 ft.) normal male and female strobili are produced. At about 4,300 feet the size and frequency of female strobili decrease. Along with the decrease in size, the strobili become increasingly deformed. The 10°C isotherm for the warmest month of the year is approximately the upper elevational limit for successful sexual reproduction of black spruce in the White Mountains of New Hampshire (Teeri, 1968). None of the female strobili above 5,000 feet was observed to release seed; in fact they usually decomposed during the growing season. Upon dissection of these cones, ¾ of the seeds were hollow or grossly deformed (Teeri, 1968).

Bisporangiate strobili occur occasionally at the elevation where female strobili start to disappear. They are borne

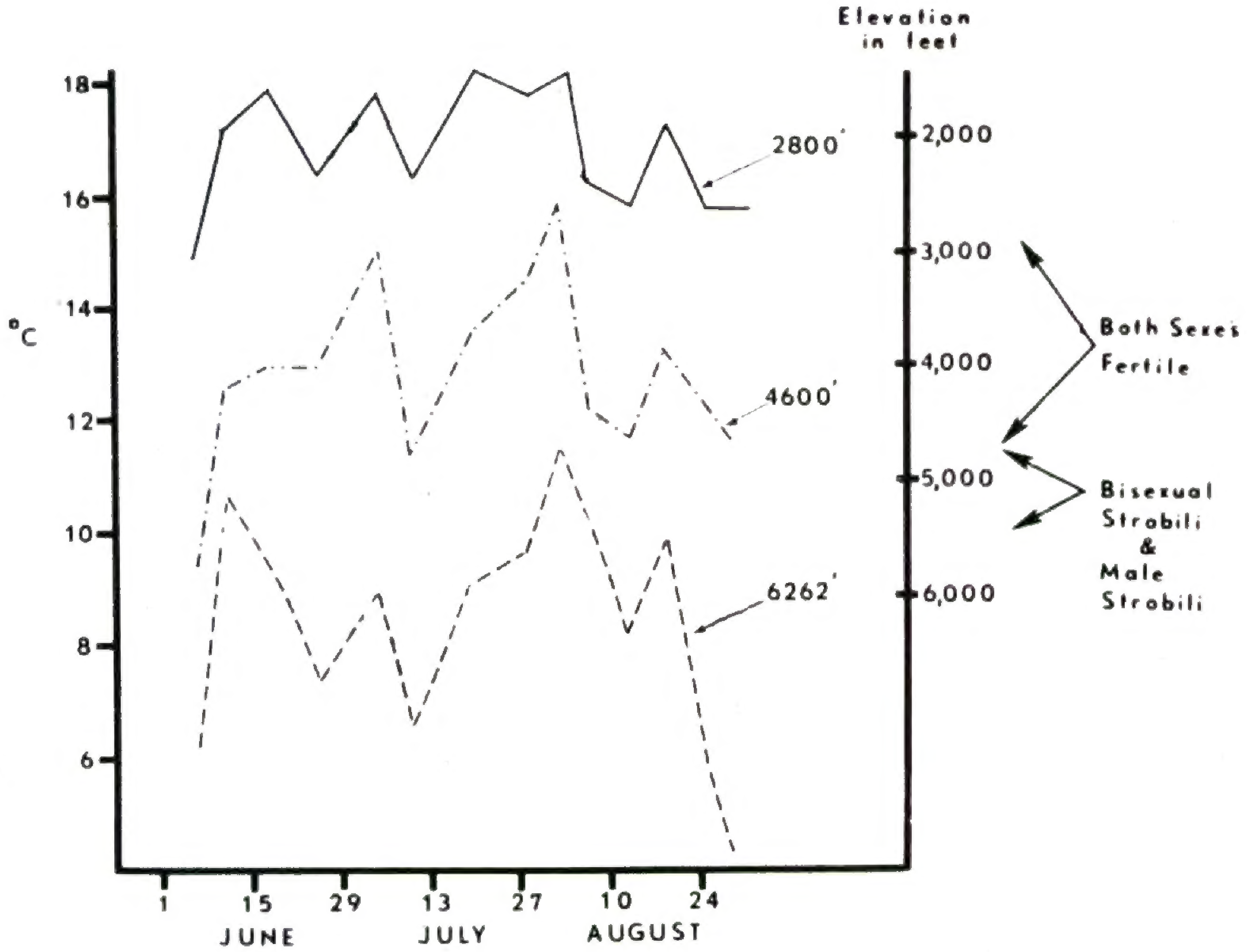

Fig. 1. Interrelations of cumulative mean air temperature at 3 elevations and fertility of subalpine black spruce. At higher elevations the bisporangiate strobili produce a small amount of fertile pollen but no viable seeds. At the same elevation male strobili produce fertile pollen, but the female strobili all appear stunted and sterile.

just below the terminal portion of new shoots (the normal position for female strobili) and are bisporangiate in one of two arrangements. In the first arrangement (longitudinally bisporangiate), the distal half of the strobilus bears ovuliferous scales, and the proximal half microsporangia (Fig. 2 A). In the second arrangement (laterally bisporangiate) the two sexes are distributed in a bilateral arrangement along the axis of the strobilus (Fig. 2 B).

The transition from male to female in the longitudinally bisporangiate strobilus is more gradual than in the laterally bisporangiate strobilus. The microsporangia in the laterally bisporangiate strobilus have already shed most of their pollen, and appear normal. The microsporophylls also seem normal (Fig. 2 B). The microsporophylls in the lower portion of the longitudinally bisporangiate strobilus

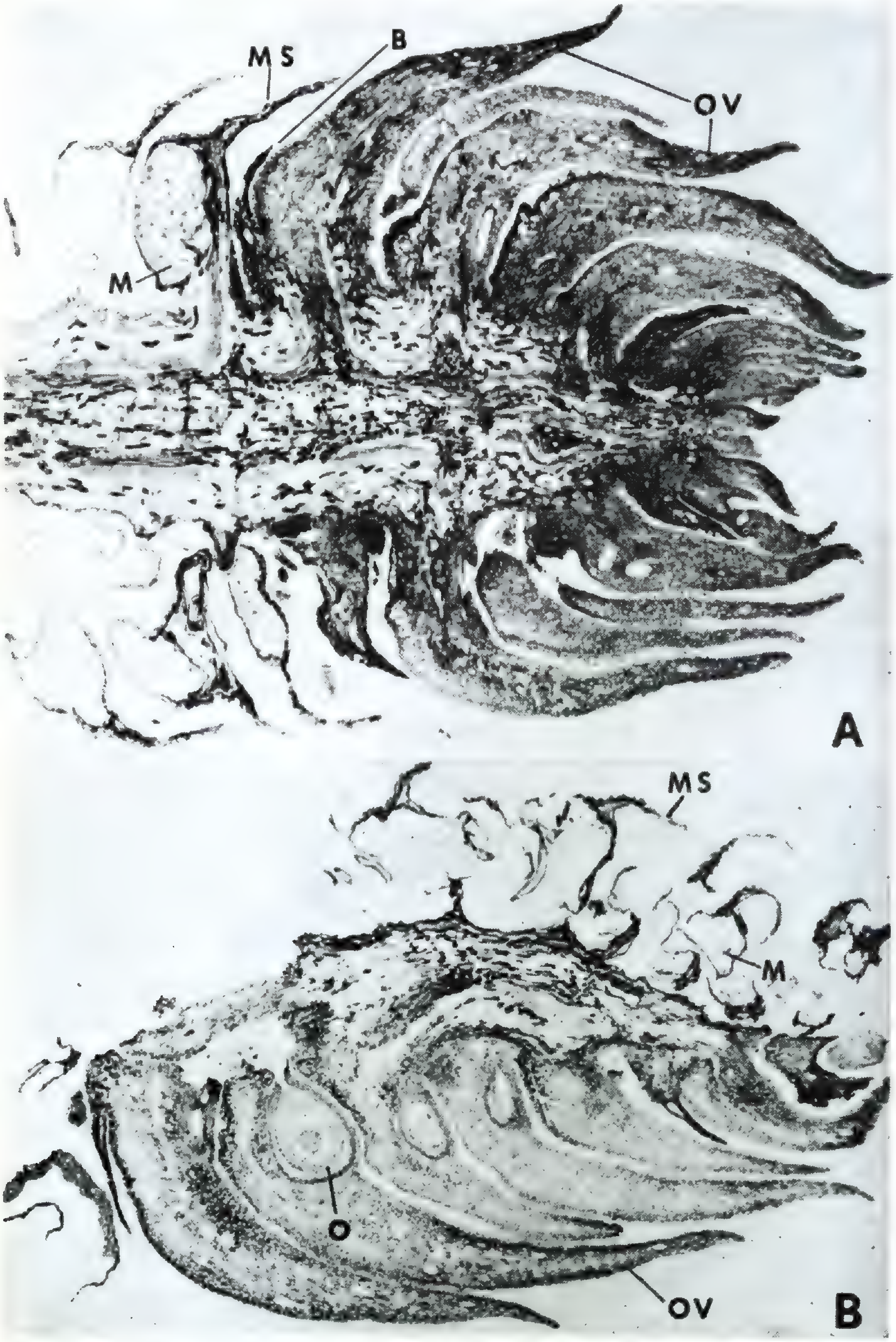

Fig. 2. Distribution of sexes in bisporangiate strobili of black spruce. A. Longitudinally bisporangiate strobilus (20×). B. Laterally bisporangiate strobilus (20×). (B) bract; (M) microsporangium; (MS) microsporophyll; (O) ovule; (OV) ovuliferous scale.

are regular in appearance and pollen in the microsporangia seems normally developed (Fig. 2 A). The ovuliferous scales in the laterally bisporangiate strobilus and the female portion of the longitudinally bisporangiate strobilus are regular in appearance. The ovules which they bear appear to be normal (no ovules are in the plane of section in Fig. 2 A) and are in the usual stage of development for conifers at pollination (Chamberlain, 1935; Foster and Gifford, 1959). Each ovule consists of a free cellular gametophyte, nucellus, and an integument that is reflexed at the micropyle to allow entry of pollen into the pollen chamber (Fig. 2 B).

Some unusual morphological characteristics are present in the transition zone between male and female portions of the longitudinally bisporangiate strobilus. The bracts subtending the ovuliferous scales in the lowermost portion of the female section often bear aborted microsporangia (B in Fig. 3 B). Bracts distal to the transition zone bear no microsporangia. Of less frequent occurrence in the transition zone are bracts that bear two microsporangia containing fully developed pollen (Fig. 3 A). The vascular tissue in the bract (or microsporophyll) exhibits the normal arrangement of xylem and phloem (phloem abaxial to the xylem), whereas the vascular tissue in the associated ovuliferous scale exhibits the typical reversal of xylem and phloem (phloem adaxial to the xylem) in the ovuliferous scale of conifers (Chamberlain, 1935; Foster and Gifford, 1959). The normal orientation of xylem and phloem indicates that the structure bearing microsporangia in Figure 3 A is a bract subtending an ovuliferous scale, and is also functioning as a microsporophyll. This unusual condition has also been reported for *Pinus* (Chamberlain. 1935).

DISCUSSION

Sexual reproduction is not common in subalpine black spruce in New England (Teeri, 1969). Reduced fertility is associated with a decrease in size of the female strobili

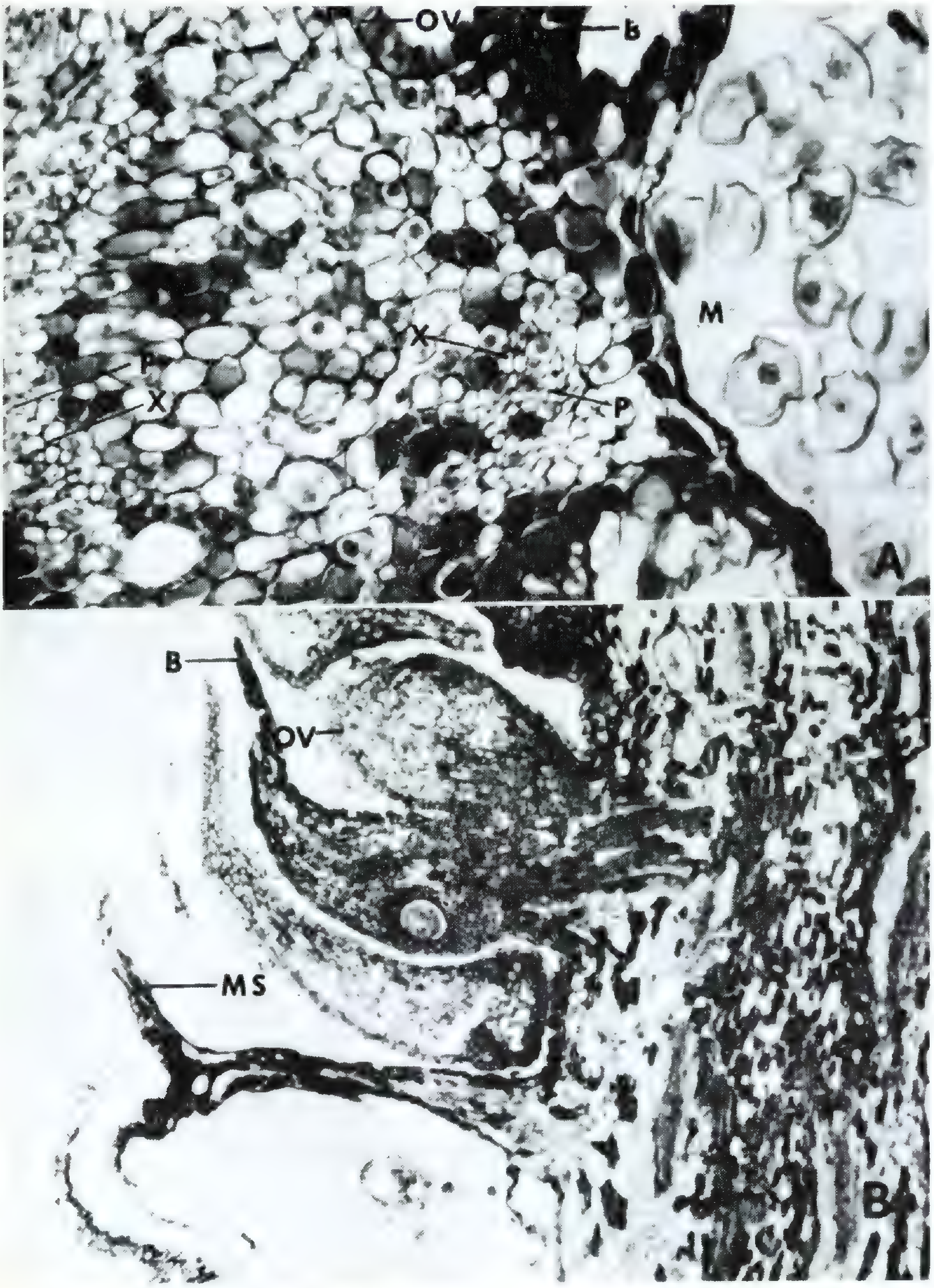

Fig. 3. A. Cross section of ovuliferous scale-bract complex with bract bearing a microsporangium containing pollen (170×). B. Longitudinal section of a bract bearing an aborted microsporangium (50×). (B) bract; (M) microsporangium; (MS) microsporophyll; (OV) ovuliferous scale; (P) phloem; (X) xylem.

and a decrease in the production of viable seed. As the elevation increases on Mt. Washington, the temperature and duration of the growing season decrease, and precipitation increases (Teeri, 1968). Thus, conditions favorable for sexual reproduction diminish with increasing elevation. The size and number of viable seeds per female strobilus decrease with increasing elevation up to timberline, whereas the male cones are affected principally above timberline. Therefore, the breakdown in sexual reproduction seems to specifically involve poor development of the female strobilus prior to pollination, and failure to produce viable seed following pollination since no viable seeds were found at high elevations.

In an extensive study on the reproduction of black spruce, Fraser (1957, 1966) determined that a heavy seed year follows a hot dry summer in the arctic and alpine ranges of the species. He found that a lack of warm dry weather prevents the build-up of reserve photosynthates necessary for a good seed crop and that more reproductive buds form during a good summer with a high carbohydrate accumulation. Thus the conditions prevailing at the time when buds are formed determine whether strobili or leaves will be produced from buds in reproductive positions along the branches. The decrease in optimum conditions for carbohydrate accumulation and strobili formation as elevation increases in the Presidential Range of New Hampshire may be responsible for a lack of reproductive bud inception and development at higher elevations.

In the genus *Abies* approximately the same number of reproductive buds is formed annually and hence inception is considered to be independent of external factors (Elis, 1970). The further development of these primordia is reported to be apparently influenced by external factors. For example, buds transitional between vegetative buds and female strobili were observed to occur in positions which would normally be occupied by buds of female strobili. These transitional buds produced either ovuliferous scales proximally and short needles distally, eventually

developing into shoots, or they produced needles proximally and subsequently developed ovuliferous scales. One bisporangiate strobilus was observed that was female in the terminal portions and male at the base.

As in *Abies*, changes in external conditions may be responsible for the production of bisporangiate strobili in black spruce. The conditions under which a strobilus begins development may favor formation of microsporophylls, while later conditions may favor the production of ovuliferous scales. The laterally bisporangiate strobilus is difficult to fit into this general explanation. If the sexual expression of a reproductive bud is controlled by a sensitive physiological balance of growth regulating substances or nutrients, this balance could be upset in a longitudinal or lateral manner at the environmental limits of the species tolerance. In the case of the longitudinally bisporangiate strobilus, either the strobilus apical meristem or the embryonic primordia that were cut off by it changed their course of development completely; whereas in the case of the laterally bisporangiate strobilus, either the strobilus apical meristem or the primordia alternate between micro- and mega-physiological states during which male and female reproductive structures are formed.

Bisporangiate strobili and abnormal positioning of female strobili have been reported for *Pinus contorta* (Black, 1961) and balsam fir (Schooley, 1967). In these cases the female and bisporangiate strobili replace male strobili in the male clusters at the base of the new shoot. These female strobili are somewhat stunted and produce a smaller number of viable seeds than do normally positioned ones. It is apparent from these studies that the position of a reproductive bud does not have complete influence on its development. The bisporangiate strobili of black spruce are also borne in positions where female strobili normally occur, but this position does not absolutely predispose the strobilus to total female expression.

The larger female strobili probably require more photosynthate for development than male strobili (Fraser,

1957), and bisporangiate strobili occur where environmental conditions are marginal for female strobilus production. Environmental extremes have been invoked elsewhere as an explanation of the sporadic occurrence of bisporangiate strobili (Black, 1961; Santamour, 1959; Elis, 1970). There are several factors that could explain why the male strobili continue to form normally at elevations where female strobili fail to complete normal development. Fraser (1966) has observed that male cones of black spruce differentiate about a week earlier than female strobili. At the end of the relatively brief growing season at timberline, the earlier onset of development of male strobili would allow a longer period for initial development. In addition, the female strobili are considerably larger than the male strobili and in the growth-limiting timberline environment, the smaller male strobili are more likely to receive the necessary photosynthate for completion of development than the larger female strobili.

Chamberlain (1935) discusses the various morphological interpretations of the bract and ovuliferous scale. He considers the bract of the female strobilus to be homologous to the microsporophyll of the male cone. The bisporangiate strobili described in this paper are teratological phenomena and any phylogenetic inferences or interpretations of homology should be drawn with considerable caution. However, the fact that bracts subtending ovuliferous scales in the transition zone of the longitudinally bisporangiate strobilus bear microsporangia tends to substantiate Chamberlain's (1935) conclusion as to the nature of the bract in the female strobilus of conifers.

SUMMARY

Bisporangiate strobili are occasionally produced on plants of black spruce at timberline (4500-4700 ft.) in the mountains of New Hampshire. These abnormal strobili occur at the upper elevational limit of production of "normal" female strobili. The air temperatures of the growing season at this elevation are near the lower limit (mean July

temperature ca. 10°C) reported for successful growth and reproduction of black spruce in other parts of its range.

The bisporangiate strobili occupy positions on the terminal portions of the branches where female strobili would normally occur. At pollination the ovules and pollen grains appear normal. Bisporangiate strobili are probably indicative of changing or adverse environmental conditions causing changes in physiological states and subsequent morphogenesis and sex expression. Bracts subtending ovuliferous scales may bear microsporangia in the transition zone between sexes in longitudinally bisporangiate strobili.

ACKNOWLEDGMENTS

We thank Dr. C. G. Nast for encouragement during the course of this investigation and Dr. R. A. White for reviewing the manuscript. We also thank Ms. T. S. Teeri for first discovering bisporangiate cones on subalpine black spruce in the White Mountains of New Hampshire and drawing them to our attention.

LITERATURE CITED

BLACK, T. M. 1961. Abnormalities of the reproductive system of *Pinus contorta* Loudon. Ann. Bot. n.s. **25**: 21-28.

CHAMBERLAIN, C. J. 1935. Gymnosperms. Structure and Evolution. University of Chicago Press. 484 p.

ELIS, S. 1970. Reproduction and reproductive irregularities of *Abies lasiocarpa* and *A. grandis*. Can. Jour. Bot. **48**: 141-143.

FOSTER, A. S., & E. M. GIFFORD, JR. 1959. Comparative Morphology of Vascular Plants. W. H. Freeman and Co., San Francisco. 555 p.

FRASER, D. A. 1957. The relation of environmental factors to flowering in spruce. *In:* K. V. THIMANN, ED. The physiology of forest trees. The Ronald Press Co., N. Y. Chapter 34.

————. 1966. Vegetative and reproductive growth of Black Spruce (*Picea mariana* (Mill.) BSP.) at Chalk River, Ontario, Canada. Can. Jour. Bot. **44**: 567-580.

RICHTER, F. I. 1932. Bisexual flowers among the pines. Jour. For. **30**: 873.

SANTAMOUR, F. S. 1959. Bisexual conelets in Spruce. Morris Arbor. Bull. **10**: 10-11.

SCHOOLEY, H. O. 1967. Aberrant ovulate cones in Balsam Fir. For. Sci. **13**: 102-104.

TEERI, J. A. 1968. The ecology of subalpine Black Spruce in New England. Masters Thesis, University of New Hampshire. 62 p.

———. 1969. The phytogeography of subalpine Black Spruce in New England. Rhodora **71**: 1-6.

ZOBEL, B. J. 1952. Abnormal cone formation in pines. Texas Jour. Sci. **4**: 517-520.

DEPT. OF BOTANY AND PLANT PATHOLOGY
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BIOSYSTEMATIC OBSERVATIONS ON APHRAGMIA INUNDATA (ACANTHACEAE) FROM MEXICO[1]

ROBERT W. LONG

The genus *Ruellia* L. (*sensu lato*) is a large group of plants that is poorly understood taxonomically, especially in the tropics, and until recently there have been few opportunities to compare the better-known North American species with those of Mexico and the American tropics. Acquisition of materials was begun a number of years ago in preparation for selected biosystematic investigations of certain wide-ranging tropical species and their relationship to North American taxa. It is now possible to begin re-evaluation of the taxonomy of some of these species.

Field and garden studies of *Aphragmia inundata* (H.B.K.) Bremek. (*Ruellia inundata* H.B.K.) were initiated in 1970. This species occurs from Mexico south into Colombia and Brazil. Plants are quite abundant locally and may form dense thickets of low shrubs. Mass collections were made in Veracruz and Yucatan, and herbarium specimens from throughout the range were examined. Transplants were grown in the experimental garden and greenhouse, cytological studies were made, and crossing experiments were performed using a number of *Ruellia* species.

MORPHOLOGICAL COMPARISONS

In nature, *Aphragmia inundata* is a ruderal subshrub found in a wide variety of habitats. Plants grow along roadsides, on open slopes or in fields, in dry or moist situations. Characteristically, the plants have woody, whitish, glabrate stems, and their grayish-puberulent leaves emit a pungent odor that has been described as goat-like. Large

[1]Contribution No. 70 from the Botanical Laboratories, University of South Florida, Tampa, Florida. Aided by a grant from the National Science Foundation GB-35231.

Figure 1. Photograph of an herbarium specimen of *Aphragmia inundata* from the Yucatan, Mexico.

numbers of flowers are produced in rather dense subcylindric cymes. Descriptions of the flower (Standley, 1930, p. 424; Leonard, 1936, p. 208; 1951, p. 77) say the corolla is light blue, but in nature and in garden culture it is, in fact, reddish or pink. Other distinctive features of the species are the swollen nodes, the glandular pubescence of the leaves, upper stem, and inflorescence, and woody, rhizomatous underground parts (see Fig. 1).

For purposes of comparison, the important morphological characteristics of *Aphragmia inundata* are contrasted with those of the wide-spread eastern North American species, *Ruellia caroliniensis* (J. F. Gmel.) Steud. and the tropical species *R. tuberosa* L. which is also the type for the genus (Table 1). These taxa of *Ruellia* were chosen for comparison because they are representative of a large section of the genus closely allied to *Aphragmia inundata* (Long, 1975). The principal differences of *A. inundata* from the other two taxa are evident in the structure of the underground parts, the morphology of the stem, the type of inflorescence, the color and morphology of the corolla, the size of the capsule, and the number of seeds per fruit. *Aphragmia inundata* is quite distinct from the other two species.

BIOSYSTEMATIC INVESTIGATIONS

The chromosome number of *Aphragmia inundata* was determined by the aceto-carmine squash method and was found to be $n = 17$ (Fig. 2). This number is identical to all counts reported for species of *Ruellia* (Grant, 1955, Long, 1963). Meiosis was normal with the formation of seventeen bivalents, normal disjunction, and the formation of abundant, fertile pollen.

Genetic testing was carried out using greenhouse-grown plants in controlled experiments. It was not possible to attempt hybridization with many *Ruellia* taxa because of differences in flowering-time, but crosses were attempted with *R. caroliniensis,* and two tropical red-flowered species, *R. macrophylla* Vahl and *R. coccinea* Vahl. Crossing failed

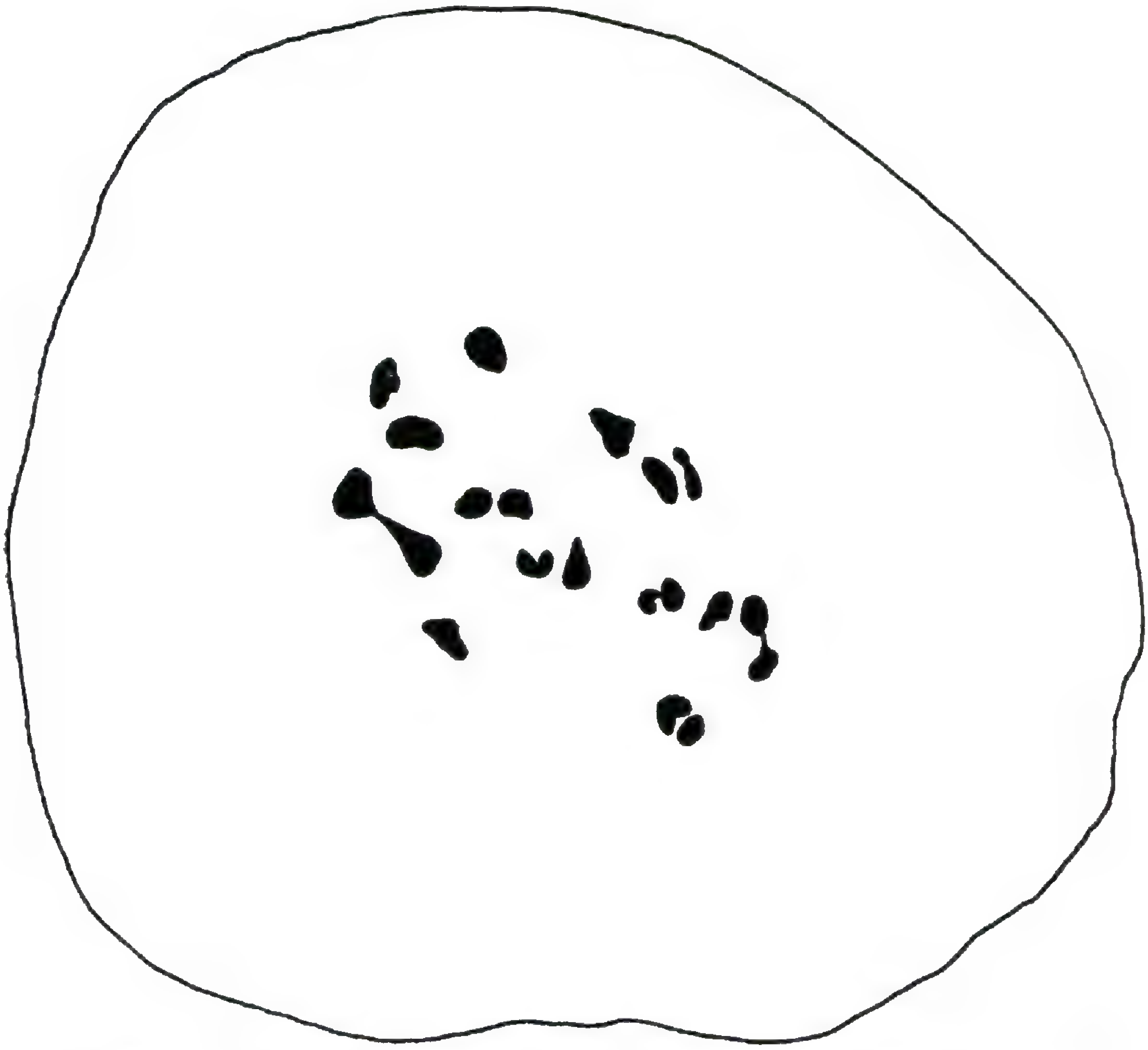

Figure 2. Meiotic chromosomes of *Aphragmia inundata*, $n = 17$, diakinesis, × 2260 approx.

in all cases after repeated attempts and thus far *A. inundata* appears to be genetically isolated from *Ruellia* taxa (Long, 1975).

There is remarkably little variation in natural populations of *Aphragmia*, with small differences between individuals. Observations on garden-grown plants showed that flowers are generally self-pollinated. The unequi-branched stigma is covered with pollen prior to anthesis. Seed set is abundant and the seeds are viable.

DISCUSSION

Bremekamp and Nannenga-Bremekamp (1948) revised the circumscription of *Ruellia* restricting the genus to five

tropical and temperate American species based on *R. tuberosa* L. as the type, and including *R. intermedia* Leonard, *R. nudiflora* (Englemann and Gray) Urban, *R. lorentziana* Griseb. and *R. malacosperma* Greenm. Bremekamp has proposed the resurrection of a number of segregate genera that were not recognized by Bentham and Hooker (1876) in their concept of the genus. He reestablished *Aphragmia* Nees (1836) based on *Ruellia inundata* H.B.K., and suggested that *Aphragmia* may include other American taxa although he made no specific recommendations. Biosystematic investigations thus far would tend to support the recognition of *Aphragmia inundata,* separating it from *Ruellia* on the basis of both morphological and genetic differences. Although *A. inundata* has the same chromosome number as species of *Ruellia,* it appears to have no close genetic relationship to *R. caroliniensis* or other species with which hybridization has been attempted. Since many *Ruellia* taxa can be successfully hybridized (Long, 1966, 1975), the fact that *A. inundata* is intersterile with species of *Ruellia* tends to support Bremekamp's separation of *A. inundata* in a different genus. Elsewhere I have discussed the necessity of revising the generic concept of *Ruellia* (Long, 1973) in the light of biosystematic research. Although Bremekamp is correct in emphasizing the unnaturalness of *Ruellia sensu lato,* his concept of *Ruellia sensu strictu* is too narrow. A number of his segregate genera, such as *Dipteracanthus* Nees and *Ulleria* Bremek. are not genetically distinct from *Ruellia,* and do not merit generic recognition (Long, 1975). The totality of evidence regarding *Aphragmia inundata,* however, based on both genetic and morphological comparisons, does support the separation of this taxon from *Ruellia.*

The taxonomy of the species is:

Aphragmia Nees in Lindl., Introd. Nat. Syst. Bot. ed. 2, p. 444, 1836, *nomen; id.* in Endl. Gen. Pl. p. 699, 1839. *emend.* Bremekamp and Nannenga-Bremekamp, Verh. Nederl. Akad. Wet. 2. 45:10. 1948.

A. inundata (H.B.K.) Brem. Verh. Nederl. Akad. Wet. **2.** 45:10. 1948. (type species)

Ruellia inundata H.B.K. Nov. Gen. et Sp. II, p. 239, 1817.

Ruellia albicaulis Bertero ex Spreng. Syst. II, p. 822, 1825.

Dipteracanthus haenkei (Nees) Nees in DC, Prodr. XI, p. 141, 1847.

Ruellia paniculata Millsp. Field Mus. Bull. **1**:46. 1895; **2**:100, 1900, *non* L.

Table 1. Morphological comparison between *Aphragmia inundata* and two species of *Ruellia*

	A. inundata	*R. caroliniensis*	*R. tuberosa*
root	knotty rhizome	fibrous, wiry roots	thickened, fusiform roots
stem	suffrutescent, simple or branched; lower stems white, glabrate, upper glandular-pilose; nodes swollen.	herbaceous, simple or divergently branching; glabrous or hirsute; nodes not swollen	herbaceous, branching; stem somewhat quadrangular, pilose or glabrate; nodes not swollen.
leaf blade	lanceolate to ovate; glandular-hispidulous	obovate, lanceolate, ovate or elliptic; hirsute to glabrate	ovate to oblong, abruptly narrowed to base; glabrous
inflorescence	dichotomously branching, in dense cylindric panicle, glandular pubescent	few-flowered glomerules, subsessile, crowded or one to few per axil.	one to several in a dichotomous cyme.
flower	corolla reddish, puberulent, tubular, 2-2.5 cm long; lobes rounded	corolla blue, lavender, or purplish, 2-5 cm long campanulate; lobes suborbicular	corolla blue, lavender, or purplish, campanulate; lobes suborbicular
fruit	glabrous; capsule 8-9 mm long, 2-4 seeded	densely pilose to glabrate; capsule 1.0-1.5 cm long, 8-seeded	glabrous; capsule 1.8-3.0 cm long, up to 40-seeded

REFERENCES

BENTHAM, G. & J. D. HOOKER. 1876. Acanthaceae. Gen. Pl. **2**: 1060-1122.

BREMEKAMP, C. E. B. & N. E. NANNENGA-BREMEKAMP. 1948. A preliminary survey of the Ruelliinae (Acanthaceae) of the Malay Archipelago and New Guinea. Verh. Nederl. Akad. Wet. 2. **45**: 1-39.

GRANT, W. F. 1955. A cytogenetic study in the Acanthaceae. Brittonia **8**: 121-149.

LEONARD, E. C. 1936. Botany of the Maya area. Miscellaneous Papers X. The Acanthaceae of the Yucatan Peninsula. Carnegie Inst. Publ. 461: 191-238.

————. 1951. The Acanthaceae of Colombia. I. Contr. U. S. Natl. Herb. **31**: 1-117.

LONG, R. W. 1963. Mass Collections of *Ruellia* in Florida. Yearbook Amer. Phil. Soc. for 1963. pp. 338-341.

————. 1966. Artificial interspecific hybridization in *Ruellia* (Acanthaceae) Amer. Jor. Bot. **53**: 917-927.

————. 1973. A biosystematic approach to generic delimitation in *Ruellia* (Acanthaceae). Taxon **22**: 543-555.

————. 1975. Artificial interspecific hydridization in temperate and tropical species of *Ruellia* (Acanthaceae). Brittonia **27**: 289-296.

STANDLEY, P. C. 1930. Flora of Yucatan. Field Museum Natural History, Botanical Series, **3**: 157-492.

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NEW PLANT RECORDS FOR THE FLORA OF LONG ISLAND, THE BAHAMAS

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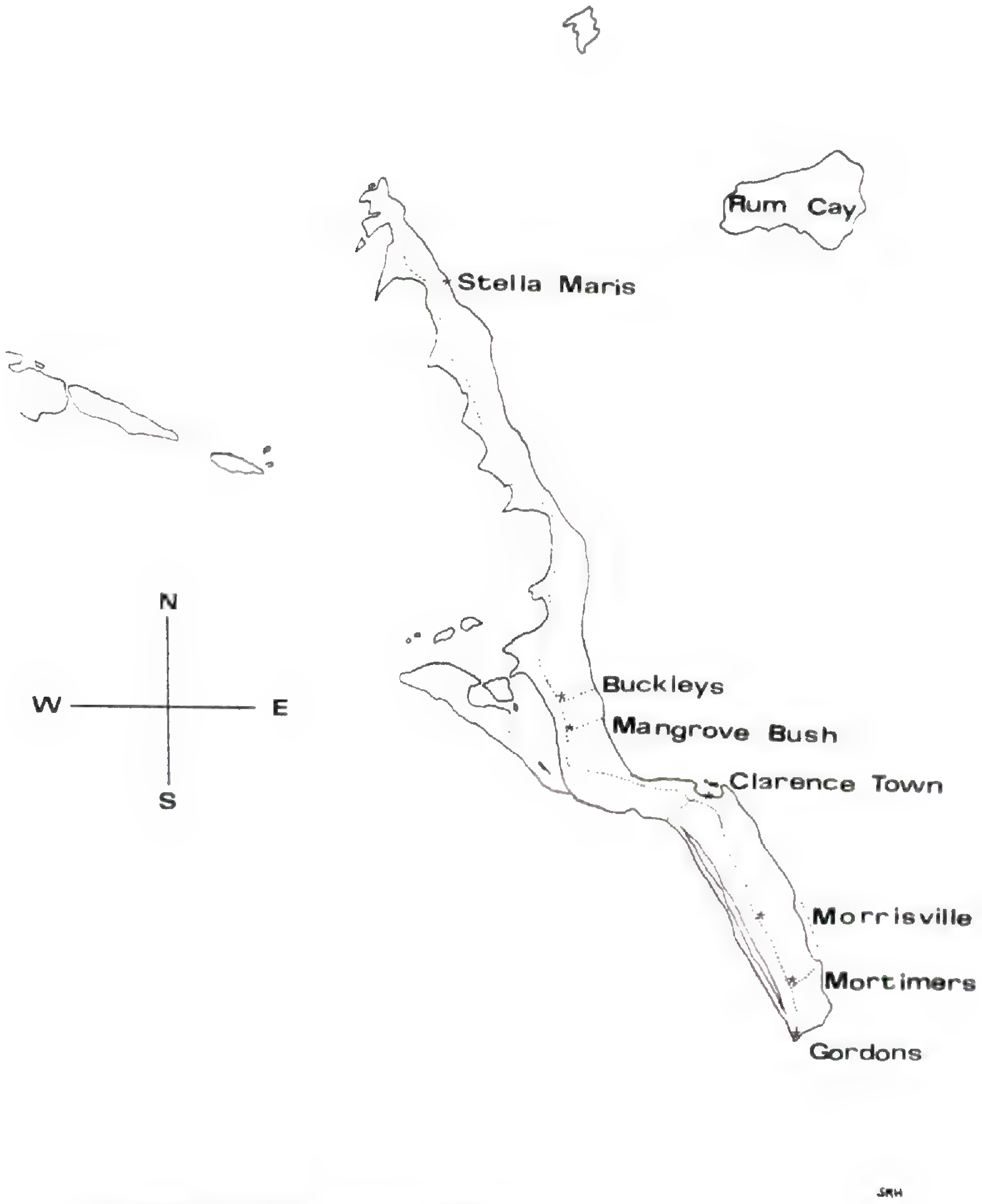
Subsequent to a recent study of the plants of Long Island, The Bahamas, (Hill, 1974) the author traveled again to the island in June and July, 1974, with the intention of further collecting. This was a particularly good time to collect on the island since it coincided with the rainy season, and most taxa were either fruiting or flowering. There are two periods of rain on Long Island, each lasting about one month, the first being in June and the second in November. There is little rain during the other months of the year, according to those residents questioned. Collections of 355 numbers were obtained during this period, mostly in sets of three. The collections have been distributed as follows: one set each to the Fairchild Tropical Garden, New York Botanical Garden, and the University of Vermont (Pringle) Herbarium. A set of the Malvaceae was sent to Dr. Paul Fryxell at Texas A & M University, the grasses were sent to Dr. Gerrit Davidse at the Missouri Botanical Garden, and the sedges were referred to Dr. Tetsuo Koyama at the New York Botanical Garden. Unless otherwise stated, the determinations were by the author.

The large number of new records reflects the fact that there have been rather few botanists on the island, despite its large size (see Hill, 1974 for further details). This series of collections was made at various points on Long Island from the southernmost point (named 'Gordon's') to a short distance from the northernmost point at Stella Maris. General collecting was done, with special attention to plants not seen in other sections of the island. The records were then carefully checked with those in the *Bahama Flora* of Britton and Millspaugh (1920), and those not known previously from the island were included in this article. In addition, an apparent new species of *Euphorbia* was dis-

covered, and will be published separately. Species have been arranged according to the order of the *Bahama Flora.*

Several brief notes are included with each new record to localize the collection site and its habitat. The basic habitats are referred to as the following: whiteland, redland, blackland, coastal sand, or waste area. In all cases, the substrate is limestone, but the amount of accumulated humus present in a given area (and thus the amount of



LONG ISLAND – BAHAMAS

moisture which can be retained) varies. As might be expected, the blacklands have a significant layer of humus which retains some moisture. The redlands have less humus, and the whitelands are comparatively humus free. Sinkholes are common in areas where humus has accumulated, since the humic acid encourages solution of the limestone. The waste areas include pastures, roadsides, agricultural lands and other disturbed areas providing suitable habitats for escapes or introduced species.

Long Island has one primary road, called the Queen's Highway, which runs the length of the island. From this road several smaller roads cut across the island at various points in order to reach the coast. These have local names. The eastern coast of the island is usually referred to as the 'North Coast' by the residents, and likewise the western coast is called the 'South Coast'. The western coast is lined with an extensive barrier beach and is the leeward side of the island.

The author would like to gratefully acknowledge the help and encouragement of Dr. Donovan Correll and Dr. William T. Gillis. He would especially like to thank Father Philip Bevan, formerly of St. Paul's Church, Clarence Town, for his assistance during the collecting trip.

ANGIOSPERMS

TYPHACEAE: *Typha domingensis* (Pers.) Kunth.: *Hill* 2433. Local in wet sinks along Queen's Highway at Stella Maris.

POTAMOGETONACEAE: *Halodule beaudettei* (Den Hartog) Den Hartog: *Hill* 2418. Colonies at entrance to salina at the north end of Clarence Town Harbor. Det.: D. Correll.

GRAMINEAE: *Paspalum blodgettii* Chapm.: *Hill* 2187. Waste area on Harbor Point, Clarence Town. Det. G. Davidse.

Paspalum laxum Lam.: *Hill* 2200. Roadside near Health Clinic, salina margin, Clarence Town. Det.: G. Davidse.

Paspalum fimbriatum HBK.: *Hill* 2214. Roadside near the Post Office, Clarence Town.

Lasiacis divaricata (L.) Hitchc.: *Hill* 2289. Redlands, shaded, ca. 1 mile west of the Queen's Highway on the Galloway Road, South Clarence Town.

Setaria geniculata (Lam.) Beauv.: *Hill* 2359. Roadside near Post Office, Clarence Town. Det.: G. Davidse.

Cenchrus echinatus L.: *Hill* 2360. Roadside near Post Office, Clarence Town. Det.: G. Davidse.

Stenotaphrum secundatum (Walt.) Kuntze: *Hill* 2191. Coastal sand near town dock, Clarence Town.

Aristida ternipes Cav.: *Hill* 2273. Pastureland in redlands, 0.5 mile north of Clarence Town. Det.: G. Davidse.

Chloris barbata Sw.: *Hill* 2149. Edge of pastureland near the western edge of the town salina, Clarence Town. Det.: G. Davidse.

Diplachne fascicularis (Lam.) Beauv.: *Hill* 2339. Forming patches in a fresh water marsh, low area north of St. Paul's Church, Clarence Town.

Leptochloöpsis virgata (Poir.) Yates: *Hill* 2281. Coastal sand at Galloway's Landing.

CYPERACEAE: *Cyperus ligularis* L.: *Hill* 2371. In sinkhole of fresh water, 0.25 mile east of Galloway's Landing near the road.

Eleocharis cellulosa Torr.: *Hill* 2340. Fresh water marsh, low area north of St. Paul's Church, Clarence Town.

Eleocharis caribaea (Rottb.) Blake: *Hill* 2315. Fresh water marsh, low area at Queen's Highway survey marker #BM 43, 1972, 2 miles south of Clarence Town. *Hill* 2341. Fresh water marsh, low area north of St. Paul's Church, Clarence Town. Both det.: D. Correll.

Fimbristylis castanea (Michx.) Vahl: *Hill* 2284. Waste area under coconut trees, Galloway's Landing. *Hill* 2314. Moist soil along Queen's Highway at survey marker #BM 43, 1972, 2 miles south of Clarence Town. Both det.: T. Koyama.

Fimbristylis cymosa R.Br. ssp. *spathacea* (Roth.) T. Koyama: *Hill* 2268. Crevices on rocky limestone barrens, vicinity of Holy Family Church, Mortimers. Det.: T. Koyama.

Fimbristylis ovata (Burm.) Kern.: *Hill* 2304. Rocky barrens east of the island ridge, 1 mile south of Clarence Town directly west of the Blue Hole in the Harbor. Det.: T. Koyama.

Scirpus robustus Pursh: *Hill* 2280. Large colony at the west end of the salina lying 1 mile west of St. Paul's Church, Clarence Town. Det.: T. Koyama.

Rynchospora cyperoides (Sw.) Mart.: *Hill* 2422. Blacklands among sabal palms, 0.5 mile south of Clarence Town, east of the road. Det.: D. Correll.

PALMAE: *Pseudophoenix sargentii* Wendl.: *Hill* 2398. Scattered on the low barrier ridge between 2-6 miles south of Galloway's Landing.

BROMELIACEAE: *Tillandsia balbisiana* Schultes: *Hill* 2305. Redlands west of the Queen's Highway at survey marker #BM 43, 1972, 2 miles south of Clarence Town.

Tillandsia circinata Schl.: *Hill* 2375. Blacklands 0.25 mile east of Galloway's Landing.

Tillandsia flexuosa Lindl.: *Hill* 2306. Redlands west of the Queen's Highway at survey marker #BM 43, 1972, 2 miles south of Clarence Town.

AMARYLLIDACEAE: *Agave indigatorum* Trel.: *Hill* 2347. Occasional in whitelands, vicinity of Morrisville School, Morrisville. Det.: H. S. Gentry.

Zephyranthes tubispatha (L'Herit.) Herbert: *Hill* 2262. Escaped and established in vicinity of St. Paul's Church, Clarence Town.

ORCHIDACEAE: *Spiranthes tortilis* (Sw.) L. C. Rich: *Hill* 2317. Sandy soil around marsh, east of Queen's Highway at survey marker #BM 43, 1972, 2 miles south of Clarence Town.

Broughtonia lindenii (Lindl.) Dressler: *Hill* 2426. Whitelands, rocky, along the trail to the south light, at Gordons.

Epidendrum altissima Schltr.: *Hill* 2366. Low epiphyte in shaded mangrove swamp, Galloway's Landing.

CASUARINACEAE: *Casuarina equisetifolia* Forst.: *Hill* 2369. Escaped and well established at Galloway's Landing.

ULMACEAE: *Trema lamarckianum* (R. & S.) Blume: *Hill* 2378. Whitelands just east of Buckley's School, Deadman's Cay. *Hill* 2442. Common on coastal ridge at Stella Maris.

MORACEAE: *Ficus aurea* Nutt.: *Hill* 2404. Locally common, rock barrens near beginning of the Mangrove Bush Road to the coast.

POLYGONACEAE: *Coccoloba krugii* Lindau: *Hill* 2344. Whitelands, vicinity of Morrisville School, Morrisville. Det.: D. Correll.

AMARANTHACEAE: *Amaranthus dubius* Mart. ex Thell.: *Hill* 2208. Waste area near St. Paul's Church, Clarence Town.

NYCTAGINACEAE: *Boerhavia coccinea* Mill.: *Hill* 2361. Waste area near Post Office, Clarence Town.

Guapira obtusata (Jacq.) Little: *Hill* 2379. Whitelands 0.5 mile east of Buckley's School, Deadman's Cay, on the road to the coast. Det.: D. Correll.

ANNONACEAE: *Annona squamosa* L.: *Hill* 2293. Escaped and established on hillsides in South Clarence Town.

CHRYSOBALANACEAE: *Chrysobalanus icaco* L.: *Hill* 2421. Bordering fresh water spring, 0.5 mile south of Clarence Town, west side of Queen's Highway.

MIMOSACEAE: *Pithecolobium mucronatum* Britt.: *Hill* 2234. Whitelands area near the westernmost town salina, 1 mile southwest of St. Paul's Church. Det.: D. Correll. This is not a new record, but it is a significant find, being the second collection of a species endemic to Clarence Town. This is a topotype.

Pithecolobium bahamensis Northrop: *Hill* 2230. Whitelands at north side of the southernmost town salina, Clarence Town.

Calliandra haematomma (Bert.) Benth.: *Hill* 2389. Very local in rocky field along road, Lower Deadman's Cay.

Neptunia plena (L.) Benth.: *Hill* 2286. In dunes, 100 meters east of the surf, Galloway's Landing.

CAESALPINIACEAE: *Tamarindus indica* L.: *Hill* 2146. Common escape. Western end of the northern town salina, Clarence Town.

Cassia sophera L.: *Hill* 2343. Roadside, vicinity of Morrisville School, Morrisville.

Caesalpinia reticulata Britton: *Hill* 2425. Whitelands, rocky, along the trail to the south light, at Gordons.

FABACEAE: *Ateleia gummifera* (Bert. ex DC.) Dietr.: *Hill* 2129. Rocky barrens, across the Queen's Highway from Holy Family Church, Mortimers. Det.: D. Correll.

Crotalaria retusa L.: *Hill* 2330. Coastal sands behind ridge, southern extension of the Turtle Cove Road, ca. 5 miles north of Clarence Town.

Crotalaria incana L.: *Hill* 2227. Waste area, 0.24 mile east of St. Paul's Church, Clarence Town.

Piscidia piscipula (L.) Sarg.: *Hill* 2443. On coastal ridge, Stella Maris. Not seen to grow south of Deadman's Cay.

Abrus precatorius L.: *Hill* 2296. Rocky hillsides near the plantation ruins, South Clarence Town.

Galactia bahamensis Urb.: *Hill* 2386. Coastal rock and sand, end of Buckleys Road, Deadman's Cay.

Rhynchosia minima (L.) DC.: *Hill* 2204. Coastal whitelands, near Harbor Point, Clarence Town.

MALPIGHIACEAE: *Triopteris jamaicensis* L.: *Hill* 2203. Whitelands near Harbor Point, Clarence Town.

Byrsonima lucida (Mill.) DC.: *Hill* 2395. Along coastal ridge, whitelands, 5 miles south of Galloway's Landing along the Diamond Crystal Salt Road.

Bunchosia glandulosa (Cav.) DC.: *Hill* 2249. Redlands, west side of the southwest town salina, Clarence Town.

EUPHORBIACEAE: *Euphorbia cyathophora* Murr.: *Hill* 2241. Roadsides, 0.5 mile west of St. Paul's Church, Clarence Town.

Euphorbia lecheoides Millsp.: *Hill* 2370. Coastal rock and sand, Galloway's Landing. This may be a new variety. Det.: D. Correll.

RHAMNACEAE: *Ziziphus taylori* (Britt.) M. C. Johnston: *Hill* 2427. Rocky land on trail to the south light, Gordons.

VITACEAE: *Cissus intermedia* A. Rich.: *Hill* 2377. On rock walls and shrubs along the Queen's Highway, Buckleys, Deadman's Cay.

MALVACEAE: *Sida ciliaris* L. var. *involucrata* (A. Rich.) Clem.: *Hill* 2261. Roadside, south side of the western town salina, 1 mile southwest of St. Paul's Church, Clarence Town. Det.: P. Fryxell.

Hibiscus brittonianus Kearney: *Hill* 2309. Redlands, 1 mile west of the Queen's Highway at survey marker #BM 43, 1972, ca. 2 miles south of Clarence Town. Det.: P. Fryxell.

Hibiscus tiliaceus L.: *Hill* 2444. Possibly an escape. Near Long Island Hardware Ltd. store, Deadman's Cay.

STERCULIACEAE: *Helicteres semitriloba* Bertero: *Hill* 2310. Redlands, 1 mile west of the Queen's Highway at survey marker #BM 43, 1972, ca. 2 miles south of Clarence Town.

Melochia pyramidata L.: *Hill* 2180. Waste areas around St. Paul's Church, Clarence Town.

Waltheria indica L.: *Hill* 2120. Waste areas 0.5 mile east of St. Paul's Church, Clarence Town.

CLUSIACEAE: *Clusia rosea* Jacq.: *Hill* 2403. Rocky barrens near beginning of the Mangrove Bush Road to the coast.

FLACOURTIACEAE: *Banara reticulata* Griseb.: *Hill* 2229. Whitelands at the north side of the southernmost town salina at Clarence Town. Det.: D. Correll.

PASSIFLORACEAE: *Passiflora cupraea* L.: *Hill* 2368. Coastal rock and sand behind ridge, Galloway's Landing.

CACTACEAE: *Harrisia brookii* Britton: *Hill* 2291. Rocky hills in South Clarence Town; fruiting specimens. This, again, is not a new record, but represents the second collection of a species endemic to the vicinity of Clarence Town. This is a topotype.

COMBRETACEAE: *Laguncularia racemosa* (L.) Gaertn.: *Hill* 2285. Mangrove area, 100 meters east of Galloway's Landing.

EBENACEAE: *Diospyros caribaea* (A.DC.) Standley: *Hill* 2384. Coastal ridge facing the ocean, end of Buckleys Road, Deadman's Cay.

LOGANIACEAE: *Spigelia anthelmia* L.: *Hill* 2388. Old field in redlands, Lower Deadman's Cay.

GENTIANACEAE: *Sabatia stellaris* Pursh: *Hill* 2396. Sandy roadside along coastal ridge, 5 miles south of Galloway's Landing on the Diamond Crystal Salt Road. Det.: D. Correll.

ASCLEPIADACEAE: *Cynanchum northropiae* (Schltr.) Alain: *Hill* 2406. Whitelands near Kentucky Springs Club, vicinity of Turtle Cove Road ca. 5 miles north of Clarence Town.

BORAGINACEAE: *Heliotropium nanum* Northrop: *Hill* 2355. Vicinity of Morrisville School in whitelands, Morrisville. *Hill* 2380. Coastal slopes in sand, end of Buckleys Road, Deadman's Cay. *Hill* 2430. Sandy area above salina margin, near beginning of trail to south light, Gordons. Det.: D. Correll.

Tournefortia poliochros Spreng.: *Hill* 2154. Scrubland at upper margin of the northern salina between Harbour Store and the Post Office, Clarence Town.

VERBENACEAE: *Bouchea prismatica* (L.) Kuntze: *Hill* 2213. Waste area near St. Paul's Church, Clarence Town. Det.: H. N. Moldenke.

Priva lappulacea (L.) Pers.: *Hill* 2150. Upper edges of the north salina at pasture edge. Clarence Town.

Phyla nodiflora (L.) Greene: *Hill* 2137. Moist sand near well by public beach, across from Health Clinic, Clarence Town.

LABIATAE: *Leonotis nepetaefolia* (L.) R. Br.: *Hill* 2209. Waste places near St. Paul's Church, Clarence Town.

SOLANACEAE: *Physalis angulata* L.: *Hill* 2210. Waste area near St. Paul's Church, Clarence Town.

BIGNONIACEAE: *Jacaranda caerulea* (L.) Griseb.: *Hill* 2405. Rock crevices at beginning of Mangrove Bush Road.

RUBIACEAE: *Catesbaea parviflora* Sw.: *Hill* 2399. In coastal sand, 1 mile south of Galloway's Landing.

Morinda citrifolia L.: *Hill* 2335. Roadside, 2.5 miles north of Clarence Town.

ASTERACEAE: *Iva imbricata* Walt.: *Hill* 2431. Coastal dunes, western beach, Gordons Landing. Det.: B. L. Turner.

Vernonia cinerea (L.) Less: *Hill* 2350. In cornfields, vicinity of Morrisville School, Morrisville. Det.: B. L. Turner.

Eupatorium lucayanum Britt.: *Hill* 2329. Rocky coastal bluff, Turtle Cove, near abandoned guesthouse, 5 miles north of Clarence Town. Det.: B. L. Turner.

Conyza canadensis L. var. *pusilla* (Nutt.) Cronquist: *Hill* 2179. Roadside near St. Paul's Rectory, Clarence Town.

Melanthera nivea (L.) Small: *Hill* 2148. Upper edge of northern salina, edge of pasture, Clarence Town. Det.: D. Correll.

Tridax procumbens L.: *Hill* 2115. Roadside, 0.5 mile east of St. Paul's Church, Clarence Town. Det.: D. Correll.

Flaveria trinervia (Spreng.) C. Mohr.: *Hill* 2351. Moist sinkhole, vicinity of the Morrisville School, Morrisville. Det.: B. L. Turner.

Emilia javanica (Burm.) C. B. Robins.: *Hill* 2352. Moist sinkhole, vicinity of Morrisville School, Morrisville. Det.: B. L. Turner.

GYMNOSPERMS

CYCADACEAE: *Zamia lucayana* Britton. This species is included in order to give further information on its range. The previous paper on the Flora of Long Island (Hill, 1974) noted its rediscovery at Turtle Cove. This author

again attempted to find other colonies of this interesting plant, and did so in three sites. *Hill* 2334 was from Turtle Cove (5 miles north of Clarence Town). *Hill* 2381 was from the Bluffs at the end of Buckleys Road, Deadman's Cay. *Hill* 2409 was from the dunes at the end of the Mangrove Bush Road. These collections along with reports from local residents suggest that the plant is found sparsely but continuously from a point just north of Clarence Town, at least to the north side of Deadman's Cay, about 15 miles to the north.

Ferns

POLYPODIACEAE: *Adiantum tenerum* Sw.: *Hill* 2288. Sinkhole, along Galloway Road 1.5 miles west of the Queen's Highway.

Thelypteris reptans (Gmel.) Morton: *Hill* 2353. Sinkhole, vicinity of Morrisville School, Morrisville.

Nephrolepis exaltata (L.) Schott: *Hill* 2373. Sinkhole, 0.25 mile east of Galloway's Landing.

SCHIZEACEAE: *Anemia adiantifolia* (L.) Sw.: *Hill* 2316. Walls of depression, east side of road near survey marker #BM 43, 1972. 2 miles south of Clarence Town. Seen also at Deadman's Cay.

Algae

CHLOROPHYCOPHYTA: *Udotea cyathiformis* Decaisne: *Hill* 2327. Clarence Town Harbor

Penicillus capitatus Lamarck: *Hill* 2326. Clarence Town Harbor.

Rhipocephalus phoenix (Ell. & Soland.) Kütz.: *Hill* 2325. Clarence Town Harbor.

Udotea flabellum (Ell. & Soland.) M. A. Howe: *Hill* 2324. Clarence Town Harbor.

Caulerpa cupressoides (West.) Ag.: *Hill* 2323. Clarence Town Harbor.

Avrainvillea nigricans Decaisne: *Hill* 2322. Clarence Town Harbor.

Acetabularia crenulata Lamour.: *Hill* 2414. Clarence Town Harbor.

Halimeda opuntia (L.) Lamour.: *Hill* 2415. Clarence Town Harbor.

Cymopolia barbata (L.) Lamour.: *Hill* 2419. Clarence Town Harbor.

PHAEOPHYCOPHYTA: *Turbinaria turbinata* (L.) Kuntze: *Hill* 2321. Clarence Town Harbor.

FUNGI

EUMYCOPHYTA: *Cladobotryum verticillatum* (Link ex S. F. Gray) S. J. Hughes: *Hill* 2319b. Parasite on *Russula*. Whitelands in humus pocket, 1 mile south of Clarence Town. Det.: C. Rogerson.

Sapedonium chrysospermum (Bulliard) Link ex Fries: *Hill* 2319a. Parasite on a bolete. Whitelands in humus pocket, 1 mile south of Clarence Town. Det.: C. Rogerson.

Scleroderma stellatum Berk.:*Hill* 2319d. In coastal sand near high tide mark. Galloway's Landing. Det.: C. Rogerson.

LITERATURE CITED

BRITTON, N. L., & C. F. MILLSPAUGH. 1920. Bahama Flora. Hafner Publishing Co., Inc. New York.

CORRELL, D. S. 1974. Flora of the Bahama Islands — new additions. Fairchild Trop. Gard. Bull. **29**: 11-15.

GILLIS, W. T. 1974. Name changes for the seed plants in the Bahama flora. Rhodora **76**: 67-138.

———, R. A. HOWARD & G. R. PROCTOR. 1973. Additions to the Bahama flora since Britton and Millspaugh — I. Rhodora **75**: 411-25.

HILL, S. R. 1974. Range extensions and new records for the Bahama flora. Rhodora **76**: 471-477.

TAYLOR, N. 1921. Endemism in the Bahama flora. Ann. Bot. **35**: 523-532.

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MISCELLANEOUS CHROMOSOME COUNTS OF WESTERN AMERICAN PLANTS — III

JAMES L. REVEAL AND RICHARD SPELLENBERG

In this series of papers, chromosome counts of randomly gathered western American plants are reported as part of the Intermountain Flora Project and the Southwest Flora Project. These reports will be presented from time to time by Reveal and various others of his colleagues or students. The present paper covers miscellaneous plants gathered by Reveal, primarily as a part of his monographic studies of *Eriogonum*, and by Spellenberg through his efforts on the Southwest Flora. Spellenberg presents some additional counts from the Pacific Northwest, California and Mexico. Most of the counts reported herein are from collections made during field work for our monographic or floristic studies, and many are from rather remote areas which have not been previously cytologically sampled. Many of the counts reported in broadly based studies such as this are first reports for a species, valuable in one respect by adding a bit of data to our understanding of the plant kingdom and in another by helping to strengthen or question relationships among species proposed through other types of studies. Equally important, our counts should confirm most others scattered in the literature, at the same time filling in gaps in the known cytogeography of a species. Those that contradict earlier counts indicate possible areas for further cytotaxonomic study, uncovering problems which might otherwise remain hidden, or suggest outright errors.

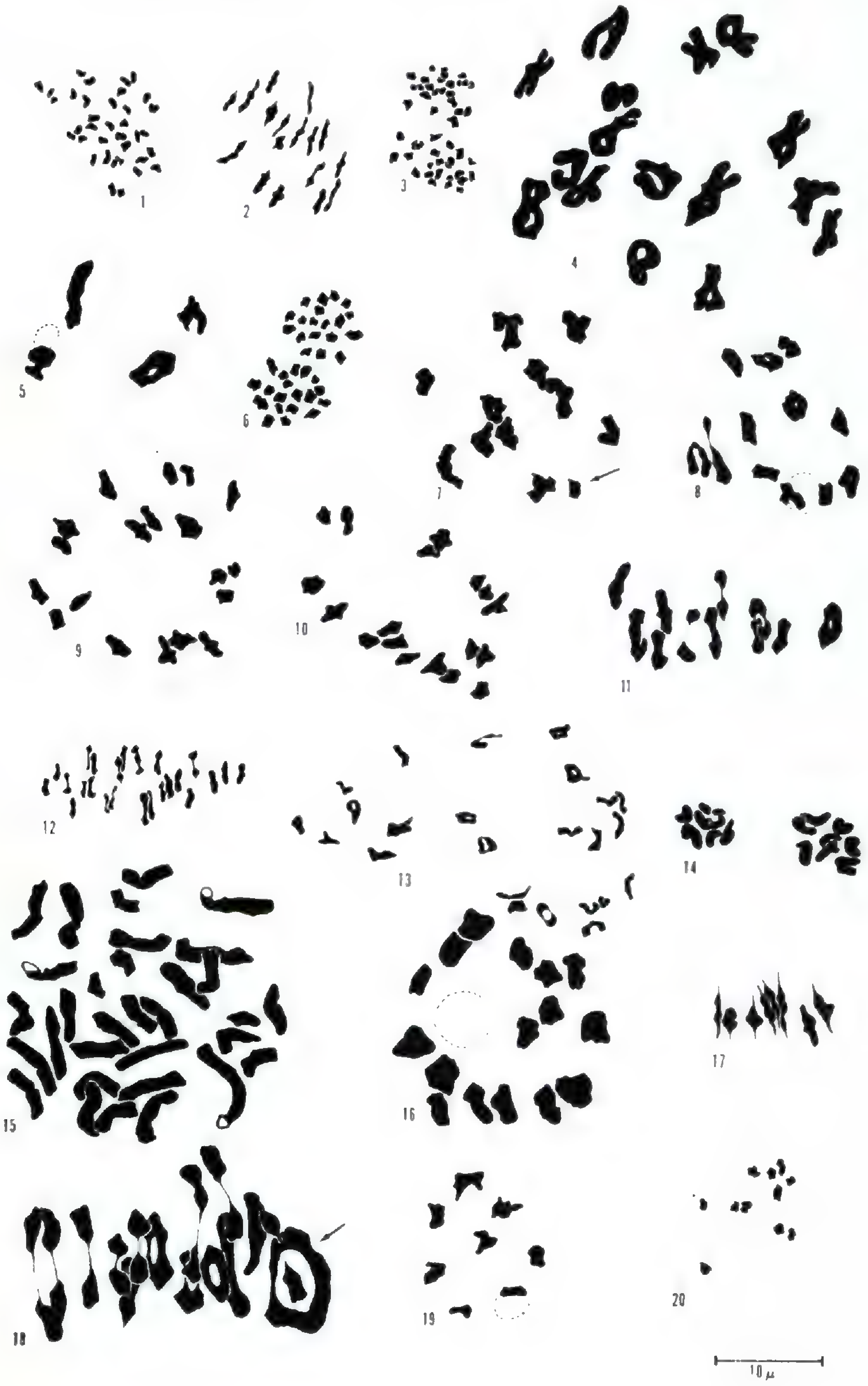
Reveal's methods for preparing his counts have been summarized in the first two parts of this series (Reveal & Styer, 1973a, 1973b). For Spellenberg, flower buds were collected from plants growing in native habitats and were fixed in modified Carnoy's solution (4 chloroform: 3 ethanol: 1 glacial acetic acid) and stored in the refrigerator. Anthers were stained and squashed according to the hy-

drochloric acid-carmine method (Snow, 1963). Mitotic counts were made from root tips of seed collected in the field and germinated on moist filter paper. They were fixed and stained by the above method except that root tips of *Carlowrightia* were first treated with an aqueous solution of paradichlorobenzene and those of *Abutilon, Menodora* and *Oxytropis* were chilled for several hours; both treatments serve to contract the chromosomes.

Chromosome numbers of 47 species and varieties are reported here. We have reviewed the standard indices for chromosome numbers and according to these sources and our knowledge of the more recently published reports, 31

LEGEND FOR FIGURES

Fig. 1: *Carlowrightia linearifolia,* $2n = 36$ — mitotic metaphase in root tip. Fig. 2: *Amaranthus palmeri,* $n = 17$ — metaphase I. Fig. 3: *Oplopanax horridum,* $n = 24$ — anaphase I. Fig. 4: *Baileya multiradiata,* $n = 16$ — diakinesis. Fig. 5: *Gutierrezia glutinosa,* $n = 4$ diakinesis. Fig. 6: *Hulsea vestita,* $n = 19$ — ½ of anaphase II configuration. Fig. 7: *Pectis angustifolia* var. *angustifolia,* $n = 12 + 1$ — diakinesis, arrow indicates a fragment or extra chromosome. Fig. 8: *Pectis papposa* var. *grandis,* $n = 12$ — diakinesis. Figs. 9, 10: *Pseudoclappia arenaria,* $n = 18$ or 19 — metaphase I. Fig. 11: *Pediocactus simpsonii* var. *robustior,* $n = 11$ — metaphase I. Fig. 12: *Lupinus concinnus* var. *concinnus,* $n = 24$ — metaphase I. Fig. 13: *Lupinus sierra-blancae,* $n = 24$ — diakinesis. Fig. 14: *Melilotus albus,* $n = 8$ — metaphase II. Figs. 15, 16: *Oxytropis lambertii* var. *bigelovii,* $2n = 32$, $n = 16$ — mitotic metaphase from root tip and diakinesis respectively. Fig. 17: *Sphaerophysa salsula,* $n = 8$ — metaphase I. Fig. 18: *Trifolium macrocephalum,* $n = 1_{IV} + 14_{II}$ — metaphase I (arrow indicates IV). Fig. 19: *Ribes bracteosum,* $n = 8$ — diakinesis. Fig. 20: *Phacelia coerulea,* $n = 11$ — diakinesis.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of the 47 counts reported here represent the first counts reported for the taxon, with those for *Carlowrightia*, *Nemacladus* and *Sphaerophysa* the first for these genera. All counts are documented by herbarium specimens. All but one of the vouchers for Reveal's counts are deposited at US, while those of Spellenberg are at NMC unless otherwise indicated by the usual herbarium abbreviation (Lanjouw & Stafleu, 1964). In the list, species for which we believe chromosome numbers are reported for the first time are preceded by an asterisk. Unless otherwise noted, all other counts confirm those reported by others. We are indebted to Norman Weatherly, an undergraduate student, for making his counts available for our use.

ACANTHACEAE

**Carlowrightia linearifolia* (Torr.) A. Gray. $2n = 36$. Fig. 1. This is believed to be the first count published for *Carlowrightia*. Many genera of Acanthaceae have a series of chromosome numbers without a common divisor. The number $n = 18$ appears several times in the family, but in light of the situation in other genera, it is not necessarily to be expected that all other species of *Carlowrightia* will have this number or be even polyploids of it. The voucher is *R. & M. Spellenberg* 1945, Doña Ana Mountains about 15 miles north of Las Cruces on a bajada south of Summerford Mountain, Doña Ana Co., New Mexico, 14 September 1968.

AMARANTHACEAE

Amaranthus palmeri S. Wats. $n = 17$. Fig. 2. This count confirms those of Grant (1958). The voucher is *Spellenberg* 2881, weed at University Ave. and Chaparral St., Las Cruces, Doña Ana Co., New Mexico, 30 June 1972.

ARALIACEAE

Oplopanax horridum (J. E. Smith) Miq. $n = 24$. Fig. 3. This count agrees with Taylor and Brockman (1966). The voucher is *R. & M. Spellenberg* 1672, Boulder Creek, about 2 miles east of Hazel, Snohomish Co., Washington, 20 May 1967.

ASTERACEAE

Baileya multiradiata Harv. & Gray. $n = 16$. Fig. 4. This report confirms those made by other investigators (see Bolkhovskikh, et al., 1969). The count, made by N. Weatherly, has as its voucher *Weatherly* s.n., 2.5 miles north of Las Cruces, Doña Ana Co., New Mexico, 7 July 1973.

Gutierrezia glutinosa (Schauer) Sch.-Bip. $n = 4$. Fig. 5. This report confirms those made by other investigators (see Bolkhovskikh, et al., 1969). The voucher is *Spellenberg* 2911, 9 miles north of U.S. Highway 70-82 on the road to Jornada del Muerto, about 12 miles north of Las Cruces, Doña Ana Co., New Mexico, 6 September 1972.

Hulsea vestita A. Gray. $n = 19$. Fig. 6. This count agrees with the count made by Raven and Kyhos (1961). The voucher is *R. & M. Spellenberg* 2878, on pumice flats 13.5 miles east of U.S. Highway 395 along California Highway 120, near the Crooked Meadows Road, Mono Co., California, 26 June 1972.

Pectis angustifolia Torr. var. *angustifolia*. $n = 12 + 1$. Fig. 7. Turner and Flyr (1966) report this entity simply as $n = 12$, but as this collection grew sympatric with *P. papposa* A. Gray var. *grandis* Keil, the irregular chromosome complement may be a reflection of possible occasional hybridization. The voucher is *Spellenberg* 2916, about 15 miles north of Las Cruces on bajada east of Summerford Mountain in the Doña Ana Mountains, Doña Ana Co., New Mexico, 22 September 1972.

Pectis papposa A. Gray var. *grandis* Keil. $n = 12$. Fig. 8. This count confirms that of several authors for *P. papposa* (see Bolkhovskikh, et al., 1969). We are not certain if any of those counts is based on a representative of this newly proposed variety. The voucher is from the same area as above, only *R. & M. Spellenberg* 2149, 14 September 1969.

Pseudoclappia arenaria Rydb. $n = 18$ or 19. Figs. 9, 10. This count is in accordance with a report of $n = 18 \pm 1$ made by Powell and Turner (1963) from a population from Reeves Co., Texas, approximately 150 miles to the southeast

of this locality. In the smears observed in our count, 19 figures were most commonly seen at metaphase 1, with 18 figures being slightly less common. In those with 19 figures however, no one figure could be certainly identified as a univalent. At other stages chromosomes tended to clump and accurate counts could not be made. An occasional anaphase I bridge was evident.

CACTACEAE

**Pediocactus simpsonii* (Engelm.) Britt. & Rose var. *robustior* (Coult.) Marshall. $n = 11$. Fig. 11. The voucher is *R. & M. Spellenberg* 1646, 13 miles west of Vantage along U.S. Highway 10, Kittitas Co., Washington, 22 April 1967.

FABACEAE

**Lupinus concinnus* Agardh. var. *concinnus*. $n = 24$. Fig. 12. The voucher is *R. & M. Spellenberg* 2977, Doña Ana Mountains, about 15 miles north of Las Cruces on a bajada west of Summerford Mountain, Doña Ana Co., New Mexico, 1 April 1973.

**Lupinus sierra-blancae* Woot. & Standl. $n = 24$. Fig. 13. The voucher is *R. & M. Spellenberg* 3345, 1 mile below ski area on Sierra Blanca, Lincoln Co., New Mexico, 8 July 1973.

Melilotus albus Lam. $n = 8$. Fig. 14. This count agrees with numerous others reported in the literature (see Bolkhovskikh, et al., 1969). The count, made by N. Weatherly, has as its voucher *Weatherly* s.n., near Doña Ana, Doña Ana Co., New Mexico, 7 July 1973.

**Oxytropis lambertii Pursh* var. *bigelovii* A. Gray. $2n = 32$. Fig. 15. The only other known count for this species is $2n = 48$ from a population of var. *lambertii* gathered in Saskatchewan (Ledingham, 1957). The voucher is *R. & M. Spellenberg* 1998, Cox Canyon, 20 miles southeast of Apache Creek, Catron Co., New Mexico, 15 October 1968. $n = 16$. Fig. 16. This voucher is *R. & M. Spellenberg* 2094, roadside at Alpine, Apache Co., Arizona, 14 August 1969.

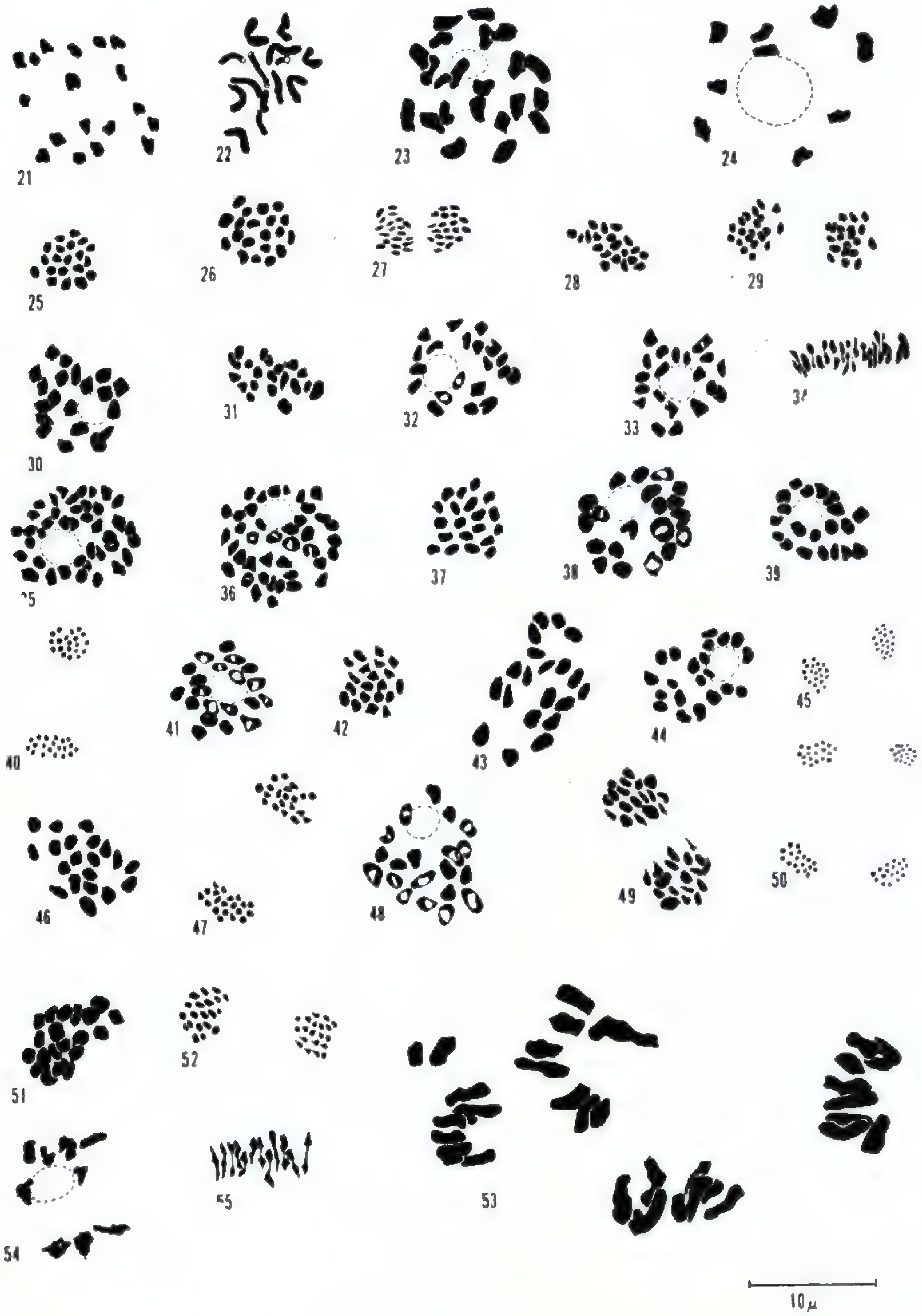
**Sphaerophysa salsula* (Pall.) DC. $n = 8$. Fig. 17. This report is believed to be the first for the genus. The species, introduced into the United States from central Asia nearly 50 years ago, commonly goes under the name of *Swainsonia salsula* (Pall.) Taub. in Engler & Prantl in floristic treatments for the western United States. Barneby (1964) recognized it as *Sphaerophysa*, where it is the typical species in the genus. *Swainsonia* in the strict sense is Australian; all counts reported for *Swainsonia* are $n = 16$ and are based on Australian and New Zealand plants (see references in Bolkhovskikh, et al., 1969). The count, made by N. Weatherly is based on *Weatherly* s.n., 3 miles north of Las Cruces, Doña Ana Co., New Mexico, 7 July 1973.

Tephrosia cana Brandeg. $n = 11$. Not figured. This count agrees with that made by Wood (1949). The voucher is *Spellenberg et al.* 3338, 2 miles east of Cabo San Lucas, Baja California Sur, Mexico, 5 June 1973.

Trifolium macrocephalum (Pursh) Poir. $n = 16$ ($1_{IV} + 14_{II}$). Fig. 18. Subsequent stages of meiosis in most cells were normal with clear counts of $n = 16$ in opposite halves of anaphase I. About 10% of the anaphase I figures, however, showed a bridge, indicating the probable presence of an inversion in addition to the translocation indicated by quadrivalent at meiosis I. Pollen from the voucher specimen has 88% of the grains stainable (counts based on 200 grains) in aniline-blue in lactophenol, indicating highly directed meiosis (Snow & Dunford, 1961). This count from a single plant gives, of course, no indication of the frequency of the translocation heterozygotes in the population, and hence the possible adaptive advantage of these heterozygotes. Snow and Dunford (1961) point out, however, that in perennial organisms with limited population size in which they must maintain a fair degree of tolerance to possible short-term unfavorable conditions, the selective advantage that might be enjoyed by the heterozygotes could be rather large. Gillett and Mosquin (1967) also report $n = 16$, ca. 16 and ca. 84 for three separate popula-

LEGEND FOR FIGURES

Fig. 21: *Nemacladus capillaris*, $n = 9$ — anaphase I. Fig. 22: *Abutilon malacum*, $2n = 14$ — mitotic metaphase from root tip. Fig. 23: *Menodora scabra*, $2n = 22$ — mitotic late prophase in root tip. Fig. 24: *Panicum sphaerocarpon*, $n = 9$ — diakinesis. Fig. 25: *Eriogonum apiculatum*, $n = 20$ — metaphase I. Figs. 26, 27: *Eriogonum batemanii*, $n = 20$ — metaphase I and anaphase I respectively. Figs. 28, 29: *Eriogonum corymbosum* var. *corymbosum*, $n = 20$ — metaphase I and anaphase I respectively. Fig. 30: *Eriogonum corymbosum* var. *glutinosum*, $n = 20$ — diakinesis. Fig. 31: *Eriogonum davidsonii*, $n = 20$ — metaphase I. Fig. 32: *Eriogonum gypsophilum*, $n = 20$ — diakinesis. Figs. 33, 34: *Eriogonum havardii*, $n = 20$ — diakinesis and metaphase I respectively. Fig. 35: *Eriogonum jamesii* var. *undulatum*, $n = 40$ — diakinesis. Fig. 36: *Eriogonum kearneyi*, $n = 40$ — diakinesis. Fig. 37: *Eriogonum lancifolium*, $n = 20$ — metaphase I. Figs. 38, 39, 40: *Eriogonum leptocladon* var. *papiliunculi*, $n = 20$ — diakinesis (38 and 39) and telophase I respectively. Figs. 41, 42: *Eriogonum leptophyllum*, $n = 20$ — diakinesis and metaphase I respectively. Fig. 43: *Eriogonum lonchophyllum*, $n = 20$ — metaphase I. Figs. 44, 45: *Eriogonum molestum*, $n = 20$ — diakinesis and anaphase I respectively. Fig. 46: *Eriogonum mortonianum*, $n = 20$ — metaphase I. Fig. 47: *Eriogonum nudum* var. *pauciflorum*, $n = 20$ — telophase I. Fig. 48: *Eriogonum pelinophilum*, $n = 20$ — diakinesis. Figs. 49, 50: *Eriogonum racemosum*, $n = 18$ — anaphase I and telophase II respectively. Fig. 51: *Eriogonum rupinum*, $n = 20$ — metaphase I. Fig. 52: *Eriogonum smithii*, $n = 20$ — late anaphase I. Fig. 53: *Delphinium amabile*, $n = 8$ — anaphase II. Fig. 54: *Lutkea pectinata*, $n = 9$ — diakinesis. Fig. 55: *Castilleja peirsonii*, $n = 12$ — metaphase I.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tions of *T. macrocephalum* located considerably to the east and south of the population counted and reported here. The presence of high polyploid on the one hand, and the observations of translocations on the other, indicate that a thorough cytogenetic study of this species throughout its range may be rewarding. The voucher for this count is *Spellenberg* 1667, 3 miles east of Virden along Washington Highway 131, Kittitas Co., Washington, 13 May 1967. (NY).

GROSSULARIACEAE

Ribes bracteosum Dougl. ex Hook. $n = 8$. Fig. 19. This count agrees with that reported by Zielinski (1953). The voucher is *R. & M. Spellenberg* 1675, 3 miles north of Barlow Pass on Mountain Loop Road, Snohomish Co., Washington, 20 May 1967 (WTU).

HYDROPHYLLACEAE

Phacelia coerulea Greene. $n = 11$. Fig. 20. The count agrees with others reported in the literature (see Bolkhovskikh, et al., 1969). The voucher is *R. & M. Spellenberg* 2978, Doña Ana Mountains, about 15 miles north of Las Cruces, on bajada west of Summerford Mountain, Doña Ana Co., New Mexico, 1 April 1973.

LOBELIACEAE

**Nemacladus capillaris* Greene. $n = 9$. Fig. 21. Chromosome numbers with a base of 9 are not particularly frequent in the Campanulaceae or Lobeliaceae, and if consistent within *Nemacladus* would further underscore the distinctness of this genus. The vouchers for this new generic count are *Spellenberg & Jackson* 2835, 5.9 miles west of Barlett Springs, Lake Co., California, 26 May 1972, which is figured, and *Spellenberg & Jackson* 2838, 2.9 miles east of Bartlett Springs, 27 May 1972, which is not figured.

MALVACEAE

**Abutilon malacum* S. Wats. $2n = 14$. Fig. 22. This count is in accordance with the diploid number reported for other species of the genus and apparently is the basic

number. The voucher is *R. & M. Spellenberg* 1950, Doña Ana Mountains, about 15 miles north of Las Cruces, on the south slope of Summerford Mountain, Doña Ana Co., New Mexico, 14 September 1968.

OLEACEAE

Menodora scabra A. Gray. $2n = 22$. Fig. 23. Lewis et al. (1962) also report $2n = 22$ for this species from a collection made in Big Bend National Park of Texas. However, Taylor (1945) reports $2n = 44$ for the same species from a collection made at the Soil Conservation Service Nursery, Tucson, Arizona. This may be another instance of different polyploid races occupying the Sonoran and Chihuahuan deserts. The voucher is *R. & M. Spellenberg* 1948, Doña Ana Mountains, about 15 miles north of Las Cruces, on the south side of Summerford Mountain, Doña Ana Co., New Mexico, 14 September 1968.

POACEAE

Panicum sphaerocarpon Ell. $n = 9$. Fig. 24. This count agrees with others (see Bolkhovskikh, et al., 1969). The voucher is *Spellenberg* 2752, 60 miles south of Tuxtepec and 39 miles north of Ixtlan de Juarez along Oaxaca Highway 175, Oaxaca, Mexico, 13 January 1972.

POLYGONACEAE

**Eriogonum apiculatum* S. Wats. $n = 20$. Fig. 25. The voucher is *Reveal & Reveal* 2861, San Jacinto Mountains, 4.4 miles north-northwest of Idyllwild along California Highway 243, Riverside Co., California, 9 August 1972.

**Eriogonum batemanii* M. E. Jones. $n = 20$. Figs. 26, 27. The voucher is *Reveal & Reveal* 2781, San Rafael Swells, along Interstate Highway 70 about 29 miles west of Green River, Emery Co., Utah, 16 July 1972.

**Eriogonum corymbosum* Benth. in DC. var. *corymbosum*. $n = 20$. Figs. 28, 29. The voucher is *Reveal & Reveal* 2875, 6.5 miles west of Mt. Carmel Junction, along Utah Highway 15, Kane Co., Utah, 12 August 1972.

**Eriogonum corymbosum* Benth. in DC. var. *glutinosum* (M. E. Jones) M. E. Jones. $n = 20$. Fig. 30. The voucher

is *Reveal & Reveal* 2887, 12 miles northeast of Henrieville, along Utah Highway 12, Garfield Co., Utah, 13 August 1972.

**Eriogonum davidsonii* Greene. $n = 20$. Fig. 31. The voucher is *Reveal & Reveal* 2862, San Jacinto Mountains, near Alandale Ranger Station, Riverside Co., California, 9 August 1972.

**Eriogonum gypsophilum* Woot. & Standl. $n = 20$. Fig. 32. This is one of the rarest species of *Eriogonum*, known only from a small number of collections. It seems to be related to the *E. brevicaule* Nutt. complex which occurs far to the north. As the name implies, it is restricted to the gypsophyllous hills which occur in the type area, but repeated searches of similar sites elsewhere have failed to reveal this plant. The voucher is *Reveal* 2949, at milepost 49.6 along U.S. Highway 285, about 16 miles north of Carlsbad, Eddy Co., New Mexico, 8 September 1972.

**Eriogonum havardii* S. Wats. Figs. 33, 34. The voucher is *Reveal* 2951, gathered in the same place as *E. gypsophilum* noted above.

Eriogonum jamesii Benth. in DC. var. *undulatum* (Benth. in DC.) Stokes ex Jones. $n = 40$. Fig. 35. This variety was previously reported by Reveal (1968) as $n = 20$ based on a collection from the Big Bend National Park of Texas. The new count, obtained from specimens further to the south indicate some cytogenetic separation that does not seem to be reinforced by morphological divergence. This is unusual for *Eriogonum* (see, for example Stebbins, 1942). The voucher is *Reveal & Hess* 2990, along the road toward Ignacio Zaragoza, about 16.5 miles southwest of Buenaventura, Chihuahua, Mexico, 10 September 1972.

**Eriogonum kearneyi* Tidestr. $n = 40$. Fig. 36. The voucher is *Reveal* 2894, 3 miles east of Pioche along Nevada Highway 85, Lincoln Co., Nevada, 15 August 1972.

**Eriogonum lancifolium* Reveal & Brotherson. $n = 20$. Fig. 37. The voucher is *Reveal* 2923, 5.5 miles east of Wellington, Carbon Co., Utah, 18 August 1972.

**Eriogonum leptocladon* Torr. & Gray var. *papiliunculi* Reveal. $n = 20$. Figs. 38, 39, 40. The vouchers for this count are *Reveal & Reveal* 2885, 10.4 miles east of Escalante along Utah Highway 12, Garfield Co., Utah, 13 August 1972 (fig. 38); *Reveal* 2906, 2.3 miles south of Page, Coconino Co., Arizona, 17 August 1972 (fig. 39); and, *Reveal* 2907 from 15 miles southeast of Page (fig. 40).

**Eriogonum leptophyllum* (Torr. & Gray) Woot. & Standl. $n = 20$. Figs. 41, 42. The voucher is *Reveal & Reveal* 2776, about 3.5 miles west of Ghost Ranch Museum along U.S. Highway 84, Rio Arriba Co., New Mexico, 15 July 1972.

**Eriogonum lonchophyllum* Torr. & Gray. $n = 20$. Fig. 43. The voucher is *Reveal* 2547, east of Durango at Squaw Creek near Fossett Gulch Road turnoff along U.S. Highway 160, La Plata Co., Colorado, 29 July 1971.

**Eriogonum molestum* S. Wats. $n = 20$. Figs. 44, 45. When the California species of *Eriogonum* were reviewed (Reveal & Munz, 1968), *E. molestum* S. Wats. was placed in synonymy with *E. nudum* Dougl. ex Benth. var. *pauciflorum* S. Wats. This was an error which cannot be placed on the shoulders of Munz, for he thought at the time it was wrong. After studying the species in the field, and once again reviewing the type, Reveal wishes to recognize that *E. molestum* is clearly a distinct species, not at all related to *E. nudum* but more closely allied with *E. davidsonii* Greene. This latter species has often been confused with *E. molestum*, and the two are closely related. In the field, they are most distinct and often grow together in the San Jacinto Mountains. The voucher for this count is *Reveal & Reveal* 2866, 6.5 miles northwest of Alandale Ranger Station along California Highway 243, San Jacinto Mountains, Riverside Co., California, 9 August 1972.

**Eriogonum mortonianum* Reveal. $n = 20$. Fig. 46. This recently proposed species has a chromosome number that is common throughout the sect. *Corymbosa*. Its voucher is *Reveal* 2904, 4.5 miles southwest of Fredonia, Mohave Co., Arizona, 16 August 1972.

**Eriogonum nudum* Dougl. ex Benth. var. *pauciflorum* S. Wats. $n = 20$. Fig. 47. The voucher is *Reveal & Reveal* 2870, 4.3 miles north-northwest of Idyllwild, San Jacinto Mountains, Riverside Co., California, 10 August 1972.

**Eriogonum pelinophilum* Reveal. $n = 20$. Fig. 48. The voucher for this count is the type of this newly proposed species, *Reveal & Reveal* 2780, 8.6 miles west of Hotchkiss, about 11.5 miles east of Delta, Delta Co., Colorado, 16 July 1972.

**Eriogonum racemosum* Nutt. $n = 18$. Figs. 49, 50. This is a most unusual number for the perennial species of *Eriogonum* as most are $n = 20$ or 40. To date, only one other member of the sect. *Racemosa* has been counted, and that species, *E. rupinum* has a chromosome number of $n = 20$ as reported below. It is suggested that *E. racemosum* will be a unique member of this species complex in this aspect, but until *E. zionis* J. T. Howell can be reported upon, the overall picture must remain somewhat vague. The voucher is *Reveal & Reveal* 2888, Cabin Hollow area just north of Red Canyon, Garfield Co., Utah, 13 August 1972. An identical count was obtained several years ago (but questioned at the time) from a collection made by *Holmgren et al.* 2202, Scofield Canyon, Grant Range, Nye Co., Nevada, 18 July 1965. It is not figured.

**Eriogonum rupinum* Reveal. $n = 20$. Fig. 51. The voucher is *Reveal* 2798, 8.2 miles north of California Highway 168 on road to Ancient Bristlecone Pine Forest, White Mountains, Inyo Co., California, 24 July 1972.

**Eriogonum smithii* Reveal. $n = 20$. Fig. 52. The voucher is *Reveal* 2921, near Big Flat Top, San Rafael Desert, Emery Co., Utah, 18 August 1972.

PRIMULACEAE

**Primula capillaris* Holmgren & Holmgren. $n = 22$. Not figured. The voucher for the count from the newly named species is the type, *Holmgren & Reveal* 2154, Thomas Creek Canyon, Ruby Mountains, Elko Co., Nevada, 15 July 1965 (UTC).

RANUNCULACEAE

**Delphinium amabile* Tidestr. $n = 8$. Fig. 53. The voucher is *R. & M. Spellenberg* 2795, below Baboquivari Peak on the lower western slopes of the Baboquivari Mountains, Pima Co., Arizona, 16 March 1972.

ROSACEAE

Lutkea pectinata (Pursh) Kuntze. $n = 9$. Fig. 54. This count agrees with the count obtained by Packer (1964). The voucher is *R. & M. Spellenberg* 1773 west of Mt. Rainier between Klapatchee Park and San Andrews Park, Mt. Rainier National Park, Washington, 22 June 1967 (NY).

SCROPHULARIACEAE

**Castilleja peirsonii Eastw.* $n=12$. Fig. 55. The voucher is *Reveal et al.* 2791, along the shore of Moon Lake, south of French Canyon, Sierra Nevada, Fresno Co., California, 21 July 1972.

LITERATURE CITED

BARNEBY, R. C. 1964. Atlas of North American species of *Astragalus*. Mem. New York Bot. Gard. **13**: 1-1188.

BOLKHOVSKIKH, Z., V. GRIF, T. MATVEJEVA, & O. ZAKHARYEVA. 1969. Chromosome numbers of flowering plants. Academy of Sciences of the USSR, Leningrad.

GILLETT, J. M., & T. MOSQUIN. 1967. *In* IOPB Chromosome number reports X. Taxon **16**: 146-157.

GRANT, W. F. 1958. Cytological aspects of sex determination and phylogenetic trends in dioecious species of *Amaranthus*. Proc. X International Congress Genetics **2**: 103.

LANJOUW, J., & F. A. STAFLEU. 1964. Index herbariorum. Part I. The herbaria of the world. Regnum Veget. vol. 31.

LEDINGHAM, G. F. 1957. Chromosome numbers of some Saskatchewan Leguminosae with particular reference to *Astragalus* and *Oxytropis*. Canad. Jour. Bot. **35**: 657-666.

LEWIS, W. H., H. L. STRIPLING & R. G. ROSS. 1962. Chromosome numbers for some angiosperms of the southern United States and Mexico. Rhodora **64**: 147-161.

PACKER, J. G. 1964. Chromosome numbers and taxonomic notes on western Canadian and Arctic plants. Canad. Jour. Bot. **42**: 473-494.

POWELL, A. M., & B. L. TURNER. 1963. Chromosome numbers in the Compositae. VII. Additional species from the southwestern United States and Mexico. Madroño **17**: 128-140.

RAVEN, P. H., & D. W. KYHOS. 1961. Chromosome numbers in Compositae. II. Helenieae. Am. Jour. Bot. **48**: 842-850.

REVEAL, J. L. 1968. Notes on the Texas eriogonums. Sida **3**: 195-205.

——— & P. A. MUNZ. 1968. "Eriogonum." *In:* P. A. MUNZ, Supplement to A California Flora. University of California Press, Berkeley.

——— & E. L. STYER. 1973a. Miscellaneous chromosome counts of western American plants — II. Great Basin Naturalist **33**: 19-25.

———. 1973b. Miscellaneous chromosome counts of western American plants — I. Southwestern Naturalist.

SNOW, R. 1963. Alcoholic hydrochloric acid — carmine as a stain for chromosomes in squash preparations. Stain Tech. **38**: 9-13.

——— & M. P. DUNFORD. 1961. A study of interchange heterozygosity in a population of *Datura meteloides*. Genetics **46**: 1097-1110.

STEBBINS, G. L. 1942. Polyploid complexes in relation to ecology and the history of floras. Am. Naturalist **76**: 36-45.

TAYLOR, H. 1945. Cyto-taxonomy and phylogeny of the Oleaceae. Brittonia **5**: 337-367.

TAYLOR, R. L., & R. P. BROCKMAN. 1966. Chromosome numbers of some western Canadian plants. Canad. Jour. Bot. **44**: 1093-1103.

TURNER, B. L., & D. FLYR. 1966. Chromosome numbers in the Compositae. X. North American species. Am. Jour. Bot. **53**: 24-33.

WOOD, C. E. 1949. The American barbistyled species of *Tephrosia*. Rhodora **51**: 193-231, 233-302, 305-364, 369-384.

ZIELINSKI, Q. B. 1953. Chromosome numbers and meiotic studies in *Ribes*. Bot. Gaz. **114**: 265-274.

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SOME SETOSE SAPROBIC PYRENOMYCETES ON OLD BASIDIOMYCETES

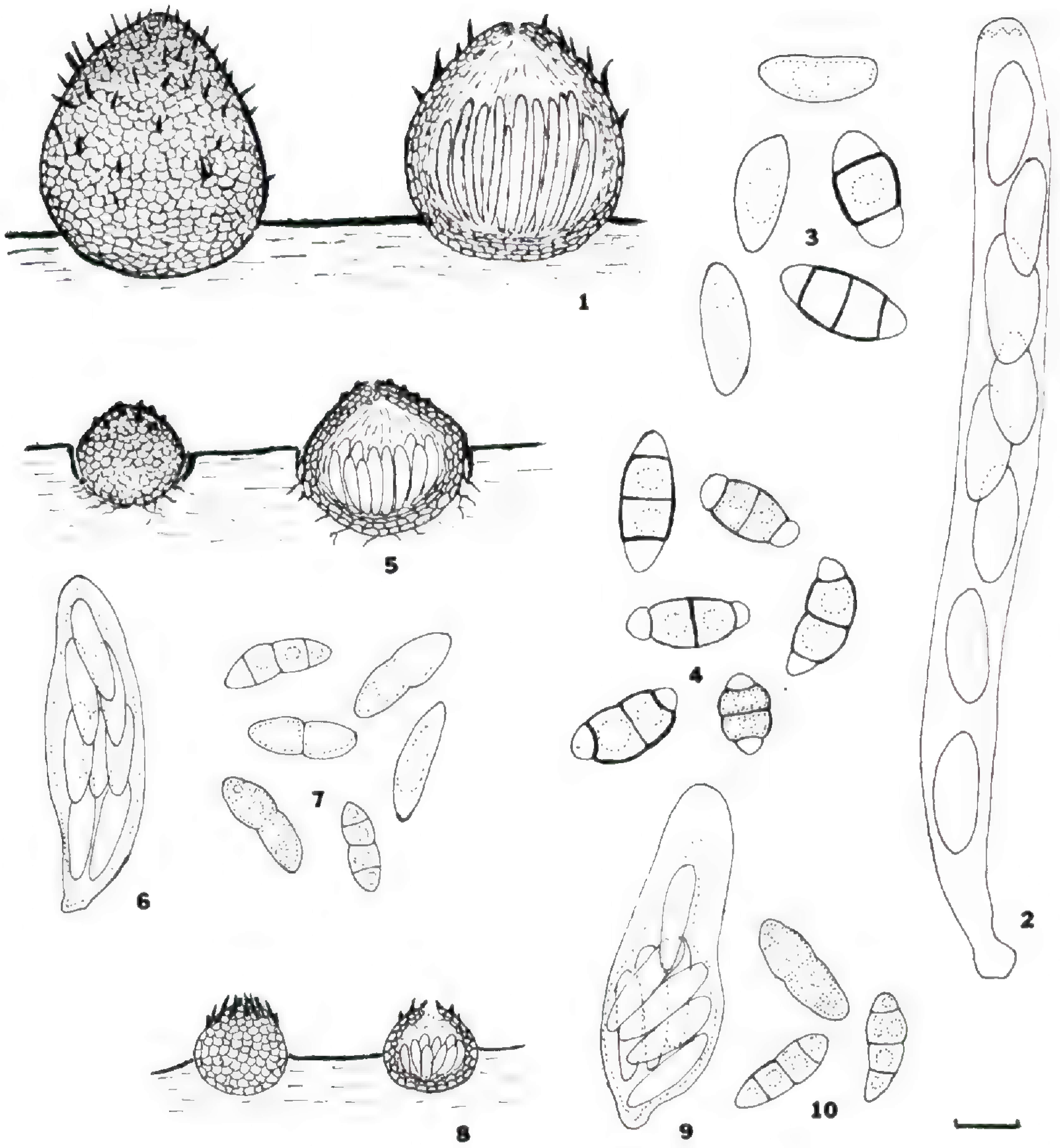
MARGARET E. BARR

Effete basidiocarps of species of thelephores and polypores serve as substrate for a number of ascomycetaceous fungi. Among these are several which have brown, three-septate ascospores, 10-17 × 3-6 μm in size, borne in dark, setose ascocarps. Recent investigations show that at least three species of Ascomycetes are involved. One species has unitunicate asci in erumpent-superficial, setose perithecia, and symmetric, elliptic ascospores the end cells of which are pallid in contrast to the dark mid cells. This species fits the concept of *Litschaueria corticiorum* (v. Höhnel) Petrak.

Litschaueria corticiorum (v. Höhnel) Petrak, Ann. Mycol. 21: 275. 1923. Figs. 1-4.

Helminthosphaeria corticiorum v. Höhnel, Sitzungsber. Kaiserl. Akad. Wiss. Math.-Naturwiss. Abt. 1, **116**: 109. 1907.

Perithecia black, immersed at first, becoming erumpent-superficial, globose ovoid, 180-330 μm diameter, 220-440 μm high, scattered or gregarious, collapsing cupulate or pinched in at sides on drying, apex short conic, pore periphysate; wall light brown in lower part, darkened toward apex, composed of several layers of compressed cells, 15-22 μm wide, bearing scattered setae over the surface, setae light to dark brown, 1-celled or septate, 40-130 μm long, 4-6 μm wide near base and tapered to pointed apex. Asci 70-110 × 6-7.5 μm, cylindric, short stipitate, unitunicate, apex rounded-truncate, apical annulus shallow, refractive, nonchitinoid, nonamyloid, asci 8-spored or less; paraphyses numerous, narrow, ca. 1 μm wide, branched and anastomosed above asci. Ascospores 10-17 × 4-6 μm, elliptic or elliptic-fusoid, symmetric, straight or inequilateral or slightly curved, (0-, 1-, 2-) 3-septate, not constricted at septa, mid cells brown, end



Figs. 1-4. *Litschaueria corticiorum:* 1. Perithecia in surface view and in section; 2. Ascus; 3. Ascospores from type collection; 4. Ascospores from North American specimens. Figs. 5-7. *Herpotrichiella porothelia:* 5. Ascocarps in surface view and in section; 6. Ascus; 7. Ascospores. Figs. 8-10. *Herpotrichiella spinifera:* 8. Ascocarps in surface view and in section; 9. Ascus; 10. Ascospores.

Standard line = 75 μm for figures 1, 5, 8; 7.5 μm for remaining figures.

cells hyaline or light brownish, with one, rarely two, globules in each cell, wall smooth, uniseriate in the ascus.

On old basidiocarps of *Peniophora, Corticium, Stereum,* and *Polyporus* spp., Europe, North America.

Material examined: EUROPE: *Peniophora cremea,* "Langenschönbickler Donauauen bei Tulln, Niederösterreich", June 1905, *v. Höhnel* (FH, type of *Helminthosphaeria corticiorum*). NORTH AMERICA: **Maine:** *Polyporus versicolor,* Flagstaff Lake Road, Franklin Co., 7 Sept 1971, *Barr* 5903b (MASS); **New York:** *Polyporus pargamenus,* woods, NE Cranberry Creek, west side Sacandaga Reservoir, Fulton Co., 1 Oct 1970, *Rogerson et al.* 70-195 (NY); **Illinois:** *Stereum ostrea,* Funk Grove, Univ. of Illinois Timber Woods, McLean Co., 13 Aug 1965, *Rogerson* (NY); **Delaware:** *Corticium* sp., Wilmington, 15 Nov 1894, *Commons* 2667 (NY); **North Carolina:** *Stereum* sp., along Toxaway River near junction with Bear Wallow Creek, Transylvania Co., 29 July 1961, *Petersen & Rogerson* (NY); *Stereum* sp., along Scotsman Creek, branch of Chattooga River, Bull Pen Road, Macon Co., 3 Aug 1961, *Petersen & Rogerson* (*Rogerson* 61-39) (NY); *Stereum* sp., along Corbin Creek, Branch of Whitewater River, Transylvania Co., 9 Aug 1961, *Petersen & Rogerson* (NY); *Stereum* sp., Lake Johnson Park, Wake Co., 12 Nov 1972, *Menge* 622 (MASS); **South Carolina:** *Stereum* sp., 3.2 miles south of state line, 4 miles south of Upper Falls of Whitewater River, Oconee Co., 14 Aug 1961, *Petersen & Rogerson* (NY, MASS).

Frequently setae similar in appearance to the perithecial setae occur scattered over the substrate surface. In the Maine collection (*Barr* 5903b) the setae on both perithecia and tubes of the substrate fungus are interspersed with conidiophores which are phialidic at the pallid apex; conidia are 9-10 $\times$ 3-3.5 μm, hyaline, elliptic-cylindric, slightly curved, 1-septate, and adhere together in small clumps. This conidial fungus agrees with the descriptions of *Cylindrotrichum oligospermum* (Corda) Bon. The connection between conidial and perithecial fungi is suggested but has been neither proved nor disproved.

The type specimen of *H. corticiorum* is rather immature, and many of the asci contain cytoplasm only. Most of those asci which appear to be mature contain one-celled brown ascospores and only a few of the ascospores are septate. This von Höhnel (1907) noted in describing the species. Petrak (1923) also described the ascospores as 0- to 1- and finally 3-septate. Von Höhnel's species is similar in all other respects to the North American specimens. There seems no doubt of the disposition of these later and better-developed collections. Both von Höhnel and Petrak compared this species with *Helminthosphaeria clavariarum* (Desm.) Fuckel. *H. clavariarum* is parasitic and forms a subiculum on species of Clavariaceae. Perithecial walls are soft and fleshy, asci have a chitinoid apical annulus, and the ascospores are one-celled with a germ pore at each end. This fungus belongs in the Sordariales (Parguay-Leduc, 1961), perhaps in its own family (Lundqvist, 1972). *Litschaueria corticiorum* on the other hand is a member of the Trichosphaeriaceae of the Xylariales.

Petrak (1940) reduced *Melanostigma* Kirschstein, with the type species *M. porothelia* (Berk. & Curt.) Kirschst., to synonymy with *Litschaueria corticiorum*, noting that Kirschstein's fungus was surely identical with von Höhnel's species, although the name *Sphaeria porothelia* Berk. & Curt. was not necessarily so. *Sphaeria porothelia* is one of the other two species which is commonly found on old basidiocarps.

The other two species have bitunicate asci in immersed or partially erumpent ascocarps, and somewhat asymmetric, inequilateral, fusoid-clavate ascospores, with all cells evenly pigmented. Of these two species, one has minute thin-walled ascocarps (95-102 μm diameter) with a tuft of short, one-celled setae at the apex around the pore region, and saccate asci 27-44 $\times$ 11.5-15.5 μm, in a fascicle in the aparaphysate locule. This fungus was described and illustrated as *Herpotrichiella spinifera* (Ell. & Ev.) Barr in Bigelow and Barr (1963). The specimens were recently re-examined, and short apical paraphyses

(periphysoids) were observed in the upper part of the locule. Such structures occur in other members of the Herpotrichiellaceae. The specimen from South Carolina cited in 1963 was incorrectly determined and is a representative of the next species. Additional collections of *H. spinifera* are now known from **Ontario:** Univ. of Toronto Exp. Forest, 8 miles south of Dorset, Haliburton Co., 8 Sept 1962, *Rogerson* 62-98 and 62-99 (NY); from **North Carolina:** Lake Johnson Park, Wake Co., 12 Nov 1972, *Menge* 622 (MASS).

The third species has somewhat thickened walls in the upper part of the larger ascocarp (104-190(-220) μm diameter), scattered protruding cells or short setae over the upper wall, and oblong asci 40-55 × 7-9 μm. Empty asci are often found in the locule and their outlines may be misinterpreted as those of pseudoparaphyses. The upper region of the locule and apical pore bear short apical paraphyses. This fungus is also a species of *Herpotrichiella* and is identical with *Sphaeria porothelia* Berk. & Curt. The species was described from *Stereum* sp., Carolina, and was sent to Berkeley by Curtis as No. 2379. The original description reads: "Perithecia minute, scattered, each seated in a little facette; sporidia uniseriate, shortly oblongo-fusiform, rather obtuse at either end, triseptate. On the hymenium of some *Stereum*. Car. Inf. No. 2379." (Berkeley 1876). From a specimen labelled "*Sphaeria Porothelia* B. & C.! Ex Herb. Curt. In Hymen Stereo" in NY, and from other collections the following description was prepared.

Herpotrichiella porothelia (Berk. & Curt.) Barr, comb. nov. Figs. 5-7.

Sphaeria porothelia Berk. & Curt. in Berk., Grevillea 4: 142. June 1876.

Melanomma porothelia (Berk. & Curt.) Sacc., Syll. Fung. 2: 104. 1883.

Leptosphaeria porothelia (Berk. & Curt.) Berl., Icones Fungorum 1: 52. 1892.

Sphaerulina porothelia (Berk. & Curt.) Keissler, Ann. Nat. Mus. Wien 35: 6. 1922.

Leptosphaeria stereicola Ellis, Am. Nat. 17: 317. Mar. 1883.

Ascocarps immersed, usually in small depressions in host tissue, about 1/3 to 1/2 erumpent, dull black, rarely more erumpent to nearly superficial, 104-190(-220) μm diameter, globose or nearly so, apex short papillate; wall brown, blackish above, of 2-3 layers of slightly compressed polygonal cells, somewhat thickened above and clypeal in aspect, with protruding cells or short 1- to 2-celled dark setae over upper part of wall; apical pore periphysoid, short apical paraphyses growing inward toward asci from apex of locule; externally at times with light brown hyphal coating extending into host tissues. Asci 40-55(-60) × 7-9 μm, oblong, slightly inflated at times, bitunicate, sessile, from sides and base of locule. Ascospores 10-14 × 3-4 μm, light dull brown, asymmetric, narrowly obovate, ends tapered, usually inequilateral, (0-, 1-, 2-) 3-septate, slightly constricted at mid septum, one globule in each cell, wall smooth, biseriate in the ascus.

In old basidiocarps of *Stereum bicolor*, *Stereum* sp., North America, Europe.

Material examined: NORTH AMERICA: **Delaware:** Newark, 7 Nov 1890, *Commons* 1722 (NY); **Iowa:** Decorah, 4 July 1882, *E. W. Holway* 142 (type specimen of *Leptosphaeria stereicola*) and three additional packets with similar collection data (one dated June 1882) (NY); **South Carolina:** Ex Herb. Curtis (authentic specimen) (NY); 3.2 mi. south of state line, 4 mi. south of Upper Falls of Whitewater River, Oconee Co., 14 Aug 1961, *Petersen & Rogerson* (with *Litschaueria corticiorum*) (NY, MASS). EUROPE: *C. Roumeguere*, Fungi sel. exs. 7356 (NY).

Ellis and Everhart (1892) distinguished *H. spinifera* with setose, partly erumpent ascocarps and shorter wider asci from *H. porothelia* (both under *Melanomma*) with glabrous, more nearly superficial ascocarps and narrower asci. The specimens of *H. porothelia* bear short setae over

the apex. For comparison, *H. spinifera* is illustrated in figures 8 to 10. These species of *Herpotrichiella* belong in the Herpotrichiellaceae of the Chaetothyriales.

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LITERATURE CITED

BERKELEY, M. J. 1876. Notices of North American Fungi. Grevillea 4: 141-162.

BIGELOW, H. E. & M. E. BARR. 1963. Contribution to the fungus flora of northeastern North America. III. Rhodora **65**: 289-309.

ELLIS, J. B. & B. M. EVERHART. 1892. The North American Pyrenomycetes. Newfield, N.J. 793 pp.

HÖHNEL, F. VON. 1907. Fragmente zur Mykologie. 112. *Helminthosphaeria Corticiorum* v. H. n. sp. Sitzungsber. Kaiserl. Akad. Wiss. Math.-Naturwiss. Abt. 1, **116**: 109-110.

LUNDQVIST, N. 1972. Nordic Sordariaceae s. lat. Symb. Bot. Upsal. **20**(1): 1-374.

PARGUAY-LEDUC, A. 1961. Étude des asques et du développement de l'*Helminthosphaeria clavariarum* (Desm.) Fuck. ap. Munk. Bull. Soc. Mycol. France **77**: 15-33.

PETRAK, F. 1923. Mykologische Notizen 257. Über *Helminthosphaeria corticiorum* v. Höhn. Ann. Mycol. **21**: 273-275.

————. 1940. Mykologische Notizen 874. Über die Gattung *Melanostigma* Kirschst. Ann. Mycol. **38**: 199.

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POLLEN SIZE OF HEDYOTIS CAERULEA (RUBIACEAE) IN RELATION TO CHROMOSOME NUMBER AND HETEROSTYLY

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Darwin (1877) observed that the Rubiaceae contain a much larger number of heterostyled genera than any other family, a fact borne out by nearly one hundred years of additional observations (Vuilleumier, 1967). Among the numerous rubiaceous taxa he examined, Darwin noted that in *Hedyotis* (*Houstonia*) *caerulea* (L.) Hooker the pollen grains from the short-styled or "thrum" flowers were larger in diameter than those from the long-styled or "pin" flowers by a ratio of as much as 100 (thrum) to 72 (pin) after soaking in water. In Darwin's sample of *H. caerulea* about 80 percent of the pollen was heteromorphic, while the remainder was similar in size regardless of style type. These observations proved generally applicable: pollen from thrum flowered plants was larger than pollen from pin flowered plants whenever there was a difference in pollen size.

In a more detailed study of heterostyly in *Oldenlandia umbellata* L., a species allied to *Hedyotis caerulea* and often placed in the same genus, Bahadur (1963) found the mean volume of pollen grains from thrum flowers to be greater (ratio about 100:79) than that of the pin pollen, as anticipated, but he also observed a wide variation in pollen size in the two flower types in different populations. In fact the overlap in size ranges was such that approximately 70 percent of the pollen could not be differentiated by size alone.

In other genera of the Rubiaceae, Bremekamp (1963) observed that of nine species of *Mapouria* seven had larger thrum pollen than pin pollen by a ratio of 100:82, but two species showed no difference in pollen size between flower

[1]I wish to thank Dr. Beryl B. Simpson, Smithsonian Institution, for her review of the manuscript.

types. He found similar results for *Psychotria* and, like Darwin, concluded that in heterostylous taxa pollen from the thrum flower is, as a rule, larger than pollen from the pin flower. But he also concluded that this difference is not always present, at least in the Rubiaceae.

I wish to consider here a phenomenon related to pollen size which has recently proved widespread among the Hedyotideae, namely, autoploidy. This phenomenon was unknown to Darwin and was not investigated by Bahadur or Bremekamp. For example, Lewis (1964, 1966) reports three cytotypes for *Oldenlandia corymbosa* L., in which the diploid race has significantly smaller pollen than the tetraploid and hexaploid races. But *O. corymbosa* is homostylous. What relation might there be between pollen size and ploidy level in heterostylous species having several chromosomal races?

Hedyotis caerulea is an ideal species for such a study; it has widespread diploid and tetraploid races (Lewis & Terrell, 1962) and is heterostylous. Consequently, flowers from herbarium sheets representing three collections of known diploid number and two collections of known tetraploid number were selected for study. Whole flowers were acetolyzed and pollen grains were mounted in glycerine jelly for measurement of equatorial and polar axes. Either 50 or, more often, 100 grains per flower were measured. The specimens used and my results are summarized in Tables 1 (diploid plants) and 2 (tetraploid plants).

Pollen of *Hedyotis caerulea* is 3-colporate with a coarsely reticulate exine (Figures 14, 15, in Lewis, 1965). In the diploid plants examined, thrum pollen is usually larger than pin pollen, i.e., the range of means $\bar{X} = 28.6\text{-}30.9$ μm (equatorial E) and $\bar{X} = 27.4\text{-}28.6$ μm (polar P), in contrast to $\bar{X} = 23.1$ μm (E) and $\bar{X} = 22.0$ μm (P) for pollen from pin flowers (*Lewis* 5605). By averaging the equatorial and polar means for each floral type the single pin pollen sample was smaller by ratios of 100:81 and 100:76 when compared with the two thrum samples. But pollen from thrum and pin flowers of *Lewis* 5613 did

Table 1.

Pollen size of the diploid race of *Hedyotis caerulea* in relation to heterostyly.

Thrum (short styled)		Pin (long styled)	
5605[1]:	28.6µm ± 1.4[2] (E) & 27.4µm ± 1.5[2] (P)	*5605:*	23.1µm ± 1.4 (E) & 22.0µm ± 2.0 (P)
3393:	30.9µm ± 2.8 (E) & 28.6µm ± 2.7 (P)		
5613:	25.2µm ± 1.7 (E) & 23.7µm ± 2.7 (P)	*5613:*	25.1µm ± 2.0[2] (E) & 25.8µm ± 2.1[2] (P)

[1]Collections (with localities): *Lewis* 5605 (Kentucky: Metcalf Co., 3.1 miles E of Wisdom, MO); *Terrell & Barclay* 3396 (Alabama: Talladega Co., 2-3 miles W of Talladega Co.-Clay Co. Line, US); *Lewis* 5613 (Arkansas: Clark Co., 2.4 miles SE of Alpine, SMU).

[2]Based on N = 50, others N = 100.

Table 2.

Pollen size of the tetraploid race of *Hedyotis caerulea* in relation to heterostyly.

Thrum (short styled)		Pin (long styled)	
3663[1]:	28.7µm ± 1.8[2] (E) & 30.2µm ± 1.6 (P)	*3663:*	23.9µm ± 1.9 (E) & 21.9µm ± 1.6 (P)
3668:	30.7µm ± 1.6 (E) & 32.1µm ± 1.7 (P)		

[1]Collections (with localities): *Terrell* 3663 (Connecticut: Tolland Co., 3 miles S of Rockville, US); *Terrell* 3668 (Vermont: Windham Co., 2 miles W of Brattleboro, US).

[2]All N = 100.

not differ significantly in size: the thrum:pin ratio was 100:104, or about equal (Table 1).

In autotetraploid plants, pollen of thrum flowers was larger than that of pin flowers, *viz.*, 100:78 (*Terrell* 3663:3663) and 100:73 (*Terrell* 3668:3663), but in approximately the same proportions and of similar size as the pollen of typical diploid plants. This contrasts to the increase in size of pollen of many tetraploids and in the closely allied but homostylous *Oldenlandia corymbosa*. Is the need for larger pollen grains among polyploids already accounted for by the typically larger grains of thrum flowers?

SUMMARY

1. Pollen from thrum flowers is typically larger than pollen from pin flowers regardless of ploidy, although for one diploid population pollen was nearly equal in size.

2. The relative size differences between pollen from thrum and pin flowers is the same whether of diploid or of tetraploid origin.

3. Pollen from diploid plants is equivalent in size to pollen of tetraploid plants in *Hedyotis caerulea*. The usually larger size of pollen grains among polyploids is not characteristic of heterostylous infraspecific polyploids.

LITERATURE CITED

BAHADUR, B. 1963. Heterostylism in *Oldenlandia umbellata* L. J. Genet. 58: 429-440.

BREMEKAMP, C. E. B. 1963. On pollen dimorphism in heterostylous Psychotrieae, especially in the genus *Mapouria* Aubl. Grana Palynol. 4: 53-63.

DARWIN, C. 1877. *The Different Forms of Flowers on Plants of the Same Species*. D. Appleton & Co., New York. 352 pp.

LEWIS, W. H. 1964. *Oldenlandia corymbosa* (Rubiaceae). Grana Palynol. 5: 330-341.

————. 1965. Pollen morphology and evolution in *Hedyotis* subgenus *Edrisia* (Rubiaceae). Amer. J. Bot. 52: 257-264.

————. 1966. Chromosome numbers of *Oldenlandia corymbosa* (Rubiaceae) from southeastern Asia. Ann. Missouri Bot. Gard. **53**: 257-258.

———— and E. E. TERRELL. 1962. Chromosomal races in eastern North American species of *Hedyotis* (*Houstonia*). Rhodora **64**: 313-323.

VUILLEUMIER, B. S. 1967. The origin and evolutionary development of heterostyly in the angiosperms. Evolution **21**: 210-226.

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RICHARD SPRUCE AND THE ETHNOBOTANY OF THE NORTHWEST AMAZON

Richard Evans Schultes

The Indians of the northwest Amazon, especially those of the Brazilian and Colombian region of the Río Vaupés, have a rich ethnopharmacological lore. This wealth of knowledge of the presumed medicinal properties of plants, however, is just coming to the fore — and most certainly not too soon, considering its disappearance in the face of advancing acculturation and the inroads of civilization.

Richard Spruce, the British plant-explorer who opened up this region to science between 1851 and 1854, must be counted amongst the greatest naturalists ever to have engaged in collecting and studies anywhere in virgin tropical territories. As a result of his meticulous observation and insatiable curiosity, a basis for our understanding of great areas of the Amazon Valley and of the northern Andes was early and most firmly laid. Not only did Spruce advance taxonomy and floristics, but he made many important observations in ethnology, linguistics and geology. Some of the most significant discoveries in connection with the hallucinogens derived from *Banisteriopsis Caapi* (Spruce ex Griseb.) Morton and *Anadenanthera* (*Piptadenia*) *peregrina* (L.) Speg. are due to his first hand field observations. And he was particularly interested in ethnobotanical lore concerning the palms (Fig. 1).

It has always been difficult for me to understand how several very important ethnobotanical discoveries eluded such a perspicacious scientist who spent four years on the Rio Negro and its tributaries. The use of *Virola* in the preparation of an hallucinogenic snuff provides a good example. Spruce gave special attention to this myristicaceous genus and collected the material on which at least nine new species were described. Although he was definitely interested in and had personal contact with several hallucinogenic plants, he failed to learn that the Indians

Figure 1. Richard Spruce. From a photograph in the Gray Herbarium. Drawn by E. W. Smith.

employed the red bark-resin of *Virola* in elaborating a snuff used by medicine men and, in some tribes, by the whole male population.

Another curious aspect of Spruce's ethnobotanical observations was his failure to discover "simples" that were employed medicinally by Indians of the northwest Amazon. "The Indians," he says, "have a few household remedies, but by far the greater portion of these have come into use since the advent of the white man from Europe and the negro from Africa." Von Martius remarks nearly the same thing in the introduction to his *Systema materiae medicae vegetabilis brasiliensis* (1843, p.xvii) . . . . "Of external applications, I have seen only the following. For a wound or bruise or swelling, the milky juice of some tree is spread thick on the skin, where it hardens into a sort of plaster, and is allowed to remain on until it falls of itself. Almost any milky tree may serve, if the juice be not acrid; but the Heveas (India-rubbers), Sapotads, and some Clusias are preferred. Such a plaster has sometimes an excellent effect in protecting the injured part from the external air."

This experience of Spruce's is difficult to reconcile with my own observations during the past 30 or more years amongst the many tribes along the Colombian Ríos Vaupés, Apaporis and Caquetá and their tributaries, where I collected large numbers of plants reputedly valuable alone or in prescriptions for a variety of common diseases.

It is true that, in this whole region, the "medicines" *par excellence* — and those which are administered not to the patient but to the medicine man — are the hallucinogens. The "medicines" with psychic properties that enable the medicine-man easily through hallucinations to see or converse with malevolent spirits from whom come all illness and death are usually far more important in native cultures than those medicines with purely physical properties. It is, however, most certainly not true that the Indians of the northwest Amazon do not possess or denigrate those medicinal plants which have properties physi-

cally to reduce pain or suffering, lessen uncomfortable symptoms of illness or even apparently cure pathological conditions. They have many such medicinal plants and are willing to share their knowledge with the serious, enquiring visitor. It is not only I who have found these people to possess a deep knowledge of medicinal plants; other botanists and several anthropologists have likewise been impressed with the wealth of native medical folklore in the region.

Spruce's surprising statements concerning the lack of knowledge and use of medicinal plants in the northwest Amazon may be explained by his difficulty in spending long periods of time with aboriginal peoples. We must always remember that Spruce was at work well over a century ago. "I have never," he wrote, "been so fortunate as to see a genuine payé [medicine-man] at work. Among the civilized Indians, the Christian padre has supplanted the pagan payé. . . . With the native and still unchristianised tribes, I have for the most part held only passing intercourse during some of my voyages. Once I lived for seven months at a time among them, on the river Vaupés, but even there I failed to catch a payé. When I was exploring the Jauarité cataracts on that river, and was the guest of Uiáca, the venerable chief of the Tucáno nation, news came . . . that a famous payé . . . would arrive that night and remain until next day, and I congratulated myself on so fine a chance of getting to know some of the secrets of his 'medicine'. . . . When he learnt that there was a white payé (meaning myself) in the village, he and his attendants immediately threw back into the canoe his goods, which they had begun to disembark, and resumed their dangerous voyage down the river in the night-time. I was told he had with him several palm-leaf boxes, containing his apparatus. . . . I could only regret that his dread of a supposed rival had prevented the interview which to me would have been full of interest; the more so as I was prepared to barter with him for the whole of his materia medica, if my stock-in-trade would have sufficed."

It is amply clear from this statement, from Spruce's reports of other ethnobotanical observations and from the rich collections of artifacts which he collected and sent to the Economic Botany Museum of the Royal Botanic Gardens at Kew that he was not — as have been a number of modern botanists working in South America's tropical regions — prejudiced against aboriginal uses of and beliefs about plants. He was certainly far from being a prejudiced man. An explanation of his failure to note the rich ethnopharmacological lore of this region may have several facets. Spruce may truly have been too busy and, much of the time, too ill to delve into this specialized field so tangential to floristic and taxonomic studies and collections. Furthermore, he may, perhaps, have erred in assuming that all "medicinal" knowledge resided with the payé, or medicine man. I have consistently found that the payé, insofar as plants are concerned, often knows relatively little about plants and usually manipulates "sacred" plants, oftentimes the hallucinogens or other psychoactive species, such as coca and tobacco, and employs them "medicinally" in magical ways. Most tribes have what we might term "regular doctors", chiefs or "curacas", who do not normally use magic and who are well provided with a general knowledge of the curative or presumed therapeutic value of plants — that is, those plants with actual physically active properties that can relieve or cure ills of the body.

They could justly be termed the botanists of the societies. They work cooperatively with the payés or medicine men, very frequently referring difficult or recalcitrant cases to these "specialists" who, naturally, are generally considered to be practitioners of a higher rank. It is, naturally, with these "regular doctors" and their knowledge that the ethnopharmacologist or ethnobotanist must primarily be involved (Fig. 2).

Whether or not in Spruce's time — a century and a quarter ago — such practitioners did not exist we cannot now state with certainty. It is, however, most probable that they did exist and did practice their skill, although perhaps

Figure 2. Makuna Indian medicine man under the influence of caapi prepared from *Banisteriopsis Caapi* (Spruce ex Griseb.) Morton. Río Popeyacá, Amazonas, Colombia. Photograph by Guillermo Cabo O.

not with so much freedom from control of the payés as today. Spruce's surmise that the few household remedies practiced amongst these peoples may have come in with Europeans or negroes is open to serious doubt, if only from the fact that the plants and uses characteristic of the household medicine of the northwest Amazon are so utterly different.

SELECTED BIBLIOGRAPHY

Altschul, Siri von Reis. 1972. The genus Anadenanthera in Amerindian cultures. Botanical Museum of Harvard University, Cambridge, Mass.

Bruzzi Alves da Silva, A. 1962. Civilizacão indígena do Uaupés. Linográfica Editôra, Ltda., São Paulo, Brazil.

García Barriga, H. 1974, 1975. Flora medicinal de Colombia; botánica médica. 2 vols. Instituto de Ciencias Naturales, Universidad Nacional, Bogotá, Colombia.

Goldman, I. 1963. The Cubeo. Illinois Studies in Anthropology, No. 2. University of Illinois Press, Urbana, Illinois.

Koch-Grünberg, T. 1909, 1910. Zwei Jahre unter den Indianern. 2 vols. Ernst Wasmuth, A.-G., Berlin, Germany.

Reichel-Dolmatoff, G. 1968. Desana. Universidad de los Andes, Bogotá, Colombia.

————. 1971. Amazonian cosmos. University of Chicago Press, Chicago, Illinois.

————. 1975. Shamanism and the jaguar. Temple University Press, Philadelphia, Pennsylvania.

Schultes, R. E. 1951. Plantae Austro-Americanae. VII. De festo seculari Ricardi Sprucei America Australi adventu commemoratio atque de plantis principaliter Vallis Amazonicis diversae observationes. Bot. Mus. Leafl., Harvard University **15**: 29-78.

————. 1953. Richard Spruce still lives. North. Gardener **7**: 20-27; 55-61; 87-93; 121-125.

————. 1961. Tapping our heritage of ethnobotanical lore. Chemurg. Digest **20**: 10-12.

————. 1962. The role of the ethnobotanist in the search for new medicinal plants. Lloydia **25**: 257-266.

————. 1967. The place of ethnobotany in the ethnopharmacologic search for psychotomimetic drugs. Pp. 33-57 *In:* D. Efron, (Ed.), Ethnopharmacologic Search for Psychoactive Drugs. Public Health Service Publ. No. 1645, U.S. Gov't Printing Office, Washington, D.C.

————. 1968. The impact of Spruce's Amazonian explorations on modern phytochemical research. Ciência e Cultura **20** (No. 1): 37-49.

————. 1968. Some impacts of Spruce's explorations on modern phytochemical research. Rhodora **70**: 313-338.

————. 1970. Foreword (pp. v-x) *In:* R. Spruce, [A. R. Wallace (Ed.)], Notes of a Botanist on the Amazon and Andes. I. [Revised edition, reprinted] Johnson Reprint Corporation, New York, N.Y.

————. 1972. From witch doctor to modern medicine. Arnoldia **32**: 198-219.

———— and B. HOLMSTEDT. 1968. De plantis toxicariis e Mundo Novo tropicale commentationes. II. The vegetal ingredients of the Myristicaceous snuffs of the northwest Amazon. Rhodora **70**: 113-160.

————, B. HOLMSTEDT, and J.-E. LINDGREN. 1969. De plantis toxicariis e Mundo Novo tropicale commentationes. III. Phytochemical examination of Spruce's original collection of *Banisteriopsis Caapi*. Bot. Mus. Leafl., Harvard Univ. **22**: 121-132.

———— and R. F. RAFFAUF. 1960. *Prestonia:* an Amazonian narcotic or not? Bot. Mus. Leafl., Harvard Univ. **19**: 109-122.

SPRUCE, R. [A. R. WALLACE Ed.]. 1908. Pp. 414-437 *In:* Notes of a Botanist on the Amazon & Andes. II. Macmillan and Co., Ltd., London, England.

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NEW COMBINATIONS IN ZANTHOXYLUM (RUTACEAE) HAWAIIAN PLANT STUDIES 44

Harold St. John

There has been much shuffling of species and varieties back and forth between *Zanthoxylum* and *Fagara.* The Hawaiian species are still in need of a monographic study, but Fosberg (1958) presented a well reasoned argument that the two groups actually had the same generic characters. On accepting this view, it is necessary to put them all in the older genus which is *Zanthoxylum* L. To have them available, the following combinations are here made.

Zanthoxylum dipetalum Mann, var. **Hillebrandii** (Sherff) comb. nov.
  Fagara dipetala (Mann) Engler, var. *Hillebrandii* Sherff, Am. Jour. Bot. 45: 462. 1958.

Z. dipetalum Mann, var. **Mannii** (Sherff) comb. nov.
  Fagara dipetala (Mann) Engler, var. *Mannii* Sherff, Am. Jour. Bot. 45: 462. 1958.

Z. hawaiiense Hbd., var. **subacutum** (Sherff) comb. nov.
  Fagara hawaiiensis (Hbd.) Engler, var. *subacuta* Sherff, Am. Jour. Bot. 45: 462. 1958.

Z. Hillebrandii Waterm., var. **hiloense** (Sherff) comb. nov.
  Fagara glandulosa (Hbd.) Engler, var. *hiloensis* Sherff, Am. Jour. Bot. 45: 462. 1958.

Z. kauaense Gray var. **kohalanum** (Sherff) comb. nov.
  Fagara kauaiensis (Gray) Engler var. *kohalana* Sherff, Am. Jour. Bot. 45: 461. 1958.

Z. kauaense Gray var. **tenuifolium** (Deg. & Sherff in Sherff) comb. nov.
  Fagara kauaiensis (Gray) Engler var. *tenuifolia* Deg. & Sherff in Sherff, Am. Jour. Bot. 45: 461. 1958.

Z. mauiense Mann var. **kaalanum** (Sherff) comb. nov.
  Fagara mauiensis (Mann) Engler var. *kaalana* Sherff, Am. Jour. Bot. 45: 462. 1958.

Z. maviense Mann var. **lanaiense** (Sherff) comb. nov.
Fagara mauiensis (Mann) Engler var. *lanaiensis* Sherff, Am. Jour. Bot. 45: 462. 1958.

Z. maviense Mann var. **maunahuiense** (Sherff) comb. nov.
Fagara mauiensis (Mann) Engler var. *maunahuiensis* Sherff, Am. Jour. Bot. 45: 462. 1958.

LITERATURE CITED

FOSBERG, F. R. 1958. *Zanthoxylum* L. and "*Xanthoxylum* Mill.", and *Thylax* Raf. Taxon 7: 94-96.

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MYRIOPHYLLUM FARWELLII (HALORAGACEAE) IN BRITISH COLUMBIA

A. CESKA AND P. D. WARRINGTON

Myriophyllum farwellii Morong. differs from all the other species of *Myriophyllum* growing (or suspected of growing) in the Pacific Northwest by its flowers in the axils of ordinary submersed leaves and in its leaves partly whorled and partly alternate. Recently (1971-1973), it has been found by us in three lakes (Echo, Mohun and Brewster) of the Campbell River area on Vancouver Island.

In these lakes it grows in the sublittoral zone, 30-120 cm below summer water level, rooted in detritic gyttja, and it is usually associated with *Scirpus subterminalis* Torr. in shallows and *Potamogeton natans* L. in deeper water. Using the Braun-Blanquet scale to indicate quantity, the two following relevés from Mohun Lake are examples of typical stands containing *M. farwellii.*

1. Depth 50 cm: *M. farwellii* 5, *Scirpus subterminalis* 2, *Potamogeton gramineus* L. +, *Utricularia vulgaris* L. +, *Nuphar polysepalum* Eng. +.

2. Depth 120 cm: *M. farwellii* 5, *Utricularia vulgaris* +, *Potamogeton natans* +.

The previously reported distribution of *Myriophyllum farwellii* was centered around the Great Lakes. In Canada *M. farwellii* occurs from Nova Scotia and New Brunswick to Ontario (Boivin, 1966), and in the United States from central New York to northern Minnesota (Muenscher, 1944; Fernald, 1950; Gleason, 1952; Fassett, 1957). Although introduction is possible, it is difficult to decide whether or not the occurrence of *M. farwellii* in British Columbia is indigenous. The distribution of vascular plants in the Pacific Northwest is not sufficiently well known and aquatic species are usually even less thoroughly collected. *Utricularia gibba* L. is an example. It was not reported from the Pacific Northwest until recently (Ceska & Bell,

1973; Hitchcock & Cronquist, 1973), although it was collected in Washington by Piper in 1897 (and misidentified as *U. minor* L.). *Sparganium fluctuans* (Morong.) Robins. was collected in British Columbia by Eastham in 1938 and has rarely been collected since. This species (with a distribution similar to that of *Myriophyllum farwellii*) has been recently collected by us in several lakes in the Campbell River area of Vancouver Island.

It is possible that *Myriophyllum farwellii* belongs to that large group of species whose distribution is disjunct due to the Continental Divide and due to the exclusion of those species from the Great Plains. Fernald (1932) discussed this problem in connection with the distribution of some species of *Potamogeton* and gave an extensive list of species with a similar distribution. Several more species (e.g., *Carex lasiocarpa* Ehrh., *Scheuchzeria palustris* L., *Brasenia schreberi* Gmel., etc.; cf. Hultén, 1964, 1971) should be added to this list.

The origin of this distributional pattern is connected with the Pleistocene history of North America (Deevey, 1949; Major & Bamberg, 1967), and the pattern is particularly pronounced in aquatic plants. Whether *Myriophyllum farwellii* really belongs to this group or whether it was introduced cannot be answered at this time.

List of localities of *Myriophyllum farwellii* and specimens collected:

1. Echo Lake (49° 59′ N., 125° 25′ W.), SW end of the lake. Collected by P. D. Warrington, September 1971; A. & O. Ceska, July 1973.
2. Mohun Lake (50° 05.3′ N., 125° 31.5′ W.), W end of the lake. Collected by O. & A. Ceska, July 1972 (*), July 1973.
3. Brewster Lake (50° 04.5′ N., 125° 35.2′ W.), S end of the lake. Collected by O. Ceska, July 1973.

Specimens are deposited in the Herbarium of the University of Victoria (UVIC), collection marked by (*) was distributed to the following herbaria: CAN, DAO, UBC, UC, and V.

ACKNOWLEDGMENTS

We thank Mrs. O. Ceska for her help in the field, W. J. Cody for the information about the representation of *M. farwellii* in the Phanerogamic Herbarium, Dept. of Agriculture, Ottawa (DAO), and that herbarium for the loan of representative specimens of *M. farwellii.* Travel expenses were partially covered by a University of Victoria Faculty Research Grant to Dr. M. A. M. Bell.

LITERATURE CITED

BOIVIN, B. 1966. Énumération des plantes du Canada. III-Herbidées, 1° partie: Digitatae: Dimerae, Liberae. Nat. Can. (Que.) **93:** 583-646.

CESKA, A., & M. A. M. BELL. 1973. *Utricularia* (Lentibulariaceae) in the Pacific Northwest. Madroño **22:** 74-84.

DEEVEY, E. S. 1949. Biogeography of the Pleistocene. I. Europe and North America. Geol. Soc. Am. Bull. **60:** 1315-1416.

FASSETT, N. C. 1957. A manual of aquatic plants. 2nd ed. Univ. of Wisconsin Press.

FERNALD, M. L. 1932. The linear-leaved North American species of *Potamogeton,* sect. Axillares. Mem. Am. Acad. Arts Sci. **17**(1): 1-183.

————. 1950. Gray's Manual of botany. 8th ed. American Book Company, New York.

GLEASON, H. A. 1952. The new Britton and Brown illustrated flora of the Northeastern United States and adjacent Canada. New York Botanical Garden.

HITCHCOCK, C. L., & A. CRONQUIST. 1973. Flora of the Pacific Northwest. An illustrated manual. Univ. of Washington Press.

HULTÉN, E. 1964. The circumpolar plants. I. Vascular cryptogams, conifers, monocotyledons. Almqvist & Wiksell, Stockholm.

————. 1971. The circumpolar plants. II. Dicotyledons. Almqvist & Wiksell, Stockholm.

MAJOR, J., & S. A. BAMBERG. 1967. Some cordilleran plants disjunct in the Sierra Nevada of California and their bearing on Pleistocene ecological conditions. Pp. 171-188 *in:* H. E. WRIGHT, JR., & W. H. OSBURN (eds.), Arctic and alpine environments. Indiana Univ. Press.

MUENSCHER, W. C. 1944. Aquatic plants of the United States. Comstock Publishing Company, Ithaca.

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REVISIONS IN THE FLORA OF ST. CROIX U.S. VIRGIN ISLANDS[1]

F. R. FOSBERG

Incidental field studies were carried out in St. Croix during a field course in tropical botany, taught at the West Indies Laboratory, Fairleigh Dickinson University. A number of plants that were not previously recorded from the island were seen, some of them collected. It seems useful to publish these records, along with corrections of the names of certain species already known from St. Croix.

There is no modern flora of St. Croix, or even an up-to-date published list. The two reasonably comprehensive source works for the St. Croix flora are Britton & Wilson, *Scientific Survey of Puerto Rico and the Virgin Islands*, volumes 5 and 6, and Little & Wadsworth, *Common Trees of Puerto Rico*. The names used by Little & Wadsworth are mostly acceptable, but only trees are included. Britton & Wilson worked under different rules of nomenclature and had much narrower generic concepts than many modern workers on tropical floras. Hence many of the names are not in accord with present usages. Dr. Alain Liogier has published a number of papers rectifying the Britton & Wilson nomenclature. His corrections are largely satisfactory, though in some cases there is room for difference of opinion.

A draft of a check-list of St. Croix plants has been prepared for use in connection with courses and research at the West Indies Laboratory (herbarium = FA). Records were extracted from the above listed works and certain others that include St. Croix plants, some of the existing herbarium material was examined, and substantial new collections were made. Included in the list also are some plants not yet represented by St. Croix specimens, but which could be reliably recorded as sight records. These

[1]West Indies Laboratory Contribution #22 (done in cooperation with the Botany Dept., U.S. National Museum of Natural History).

are mainly garden plants. This check-list is not yet completed, and it may be some time before it is, as much more collecting should be done to get a documented record of what is growing on the island at present.

Pending the completion of the check-list it seemed worthwhile to extract from it all names differing from those accepted in the Britton & Wilson and Little & Wadsworth books. As the list stands it includes accepted changes and new records of St. Croix plants from Alain's work, as well as my own new records and taxonomic changes. This extracted list is here presented as an interim source of what seem to be the correct names of St. Croix plants. Species known from the island but not included here are mostly listed under acceptable names in one of the two books cited above. Taxa not native to the island are indicated by an asterisk.

Abbreviations of principal sources are as follows:

B. & W. = Britton, N. L. and Wilson, P. Scientific Survey of Porto Rico and the Virgin Islands, vols. 5 & 6, Botany.

L. & W. = Little, E. L. and Wadsworth, F. Common trees of Puerto Rico.

Herbarium symbols are those of Index Herbariorum, ed. 6, except that FA is used for the herbarium of the Fairleigh Dickinson University West Indies Laboratory and FO is for material not yet distributed by F. R. Fosberg.

PTERIDOPHYTA

PALTONIUM Presl

Paltonium lanceolatum (L.) Presl — Bodkin Hill, *Hayes* 31 (FA).

POLYPODIUM L.

Polypodium aureum L. — Coble, 50 m, *Hayes* 47 (FA); Eliza's Retreat, in thick woods on precipitous east-facing slope, 500′, *Fosberg & Hayes* 54158 (US).

Polypodium phyllitidis L. — Bodkin Hill, 150 m, *Hayes* 29 (FA).

Polypodium polypodioides (L.) — Watt. Bodkin, 200 m, *Hayes* 41 (FA).

PTERIS L.

*Pteris longifolia L. — Christiansted, in crevices in walls and rocky waste places. *Fosberg* 53935 (US, FA); *Hayes* 27 (FA).

THELYPTERIS Schmid. (*Dryopteris* sensu B. & W. as to St. Croix records, non Adans.)

Thelypteris dentata (Forsk.) E. St. J. (*Dryopteris dentata* (Forsk.) C. Chr., B. & W. **6**: 471).

Thelypteris patens (Sw.) Small (*Dryopteris patens* (Sw.) O. Ktze., B. & W. **6**: 471).

Thelypteris poiteana (Bory) Proctor (*Dryopteris poiteana* (Bory) Urb., B. & W. **6**: 473). Spring Garden, 100 m., *Hayes* 26 (FA). Looks much like a *Tectaria* except for venation; bears plantlets on midrib of frond.

Thelypteris tetragona (Sw.) Small (*Dryopteris subtetragona* (Link) Maxon, B. & W. **6**: 473).

CYCADACEAE

*CYCAS L.

*Cycas circinalis L. — Seen planted in Christiansted, 1972.

*Cycas revoluta Thunb. — Teague Bay, planted at West Indies Laboratory, *Hayes* 134 (FA).

CUPRESSACEAE

*THUJA L.

*Thuja orientalis L. — Seen planted, 1972.

ARAUCARIACEAE

*ARAUCARIA Juss.

*Araucaria heterophylla (Salisb.) Franco. — Seen planted, 1972.

PODOCARPACEAE

*PODOCARPUS Pers.

*Podocarpus macrophyllus var. maki Endl. — Teague Bay, West Indies Lab. *Hayes* 143 (FA).

TYPHACEAE

TYPHA L.

Typha domingensis (Pers.) Kunth (*Typha angustifolia* sensu B. & W. non L., B. & W. 5: 9). Fide Alain, Rhodora 67: 317, 1965.

POTAMOGETONACEAE

(Incl. Zannichelliaceae and Ruppiaceae)

HALODULE Endl.

Halodule wrightii Aschers. (B. & W. 5: 12; *Halodule beaudettei* (d. Hart.) d. Hart.). Reported by den Hartog, Blumea 12: 303, 1964, as *H. beaudettei,* which does not seem specifically distinct from the widespread *H. wrightii.*

SYRINGODIUM Kütz.

Syringodium filiforme Kütz. (*Cymodocea manatorum* Aschers., B. & W. 5: 12).

ALISMATACEAE

ECHINODORUS Rich.

Echinodorus berteroi (Spreng.) Fassett (*Echinodorus cordifolius* Griseb., B. & W. 5: 14).

GRAMINEAE

ANDROPOGON L. (sensu lato; *Amphilophis* Nash, *Schizachyrium* Nees.).

Andropogon gracilis Spreng. (*Schizachyrium gracile* (Spreng.) Nash, B. & W. 5: 24).

Andropogon ischaemum L. (*Amphilophis ischaemum* (L.) Nash, B. & W. 5: 27).

*Andropogon pertusus (L.) Hitchc. — Reported by Hitchcock, Man. Grasses W.I., 402, 1936; now very abundant, locally called "hurricane grass."

Andropogon semiberbis Spreng. (*Schizachyrium semiberbe* (Spreng.) Nash, B. & W. 5: 25).

*BAMBUSA Retz. (*Bambos* Retz.).

*Bambusa vulgaris Schrad. (*Bambos vulgaris* Schrad., B. & W. 5: 77).

CHLORIS Sw.

*Chloris gayana Kunth — Seen persisting in old Experiment Station grounds, near Upper Bethlehem, 1972.

Chloris inflata Link (*Chloris paraguaiensis* Steud., B. & W. 5: 67; 6: 232; *Chloris barbata* sensu American authors, non (L.) Sw.) Teague Bay, *D. Smith* 11 (FA).

Chloris sagraeana A. Rich. — Said by Alain, Rhod. 67: 319, 1965, not to be in St. Croix.

CYNODON L. C. Rich. (*Capriola* Adans.).

Cynodon dactylon (L.) Pers. (*Capriola dactylon* (L.) O. Ktze., B. & W. 5: 66). Teague Bay, *Kaufman* 64 (FA).

DIGITARIA Heist. (*Syntherisma* Walt., *Valota* Adans.).

Digitaria ciliaris (Retz.) Koel. (*Syntherisma sanguinalis* sensu B. & W., non (L.) Dulac, B. & W. 5: 33).

Digitaria horizontalis Willd. (*Syntherisma digitata* (Sw.) Hitchc., B. & W. 5: 34).

Digitaria insularis (L.) Mez (*Valota insularis* (L.) Chase, B. & W. 5: 32).

Digitaria ischaemum (Schreb.) Schreb. (*Syntherisma ischaemum* (Schreb.) Nash, B. & W. 5: 33).

ERAGROSTIS Host.

*Eragrostis tenella (L.) Beauv. (*Eragrostis amabilis* (L.) W. & A., B. & W. 5: 75; 6: 332).

LASIACIS (Griseb.) Hitchc.

Lasiacis patentiflora Hitchc. & Chase. — Reported by Alain, Rhodora 67: 318, 1965.

LEPTOCHLOA Beauv. (*Diplachne* Beauv.).

Leptochloa fascicularis (Lam.) Gray (*Diplachne fascicularis* (Lam.) Beauv., B. & W. 5: 72; 6: 332).

Leptochloa panicea (Retz.) Ohwi (*Leptochloa filiformis* (Lam.) Beauv., B. & W. 5: 71). Fide Alain, Rhodora, 67: 319, 1965.

OPLISMENUS Beauv.

Oplismenus setarius (Lam.) R. & S. Reported by Hitchcock, Man. Grasses W.I. 324, 1936.

PANICUM L.

Panicum capillare L. — Reported by Hitchcock, Man. Grasses W.I. 255, 1936.

*Panicum muticum Forsk. (*Panicum purpurascens* Raddi; *Panicum barbinode* Trin.; *Brachiaria mutica* (Forsk.) Stapf).

PASPALUM L.

Paspalum distichum L. (*Paspalum vaginatum* Sw., B. & W. 5: 40). The Linnean specimen of *P. distichum* is clearly the plant commonly called *P. vaginatum* Sw.

Paspalum laxum Lam. (*Paspalum glabrum* Poir., B. & W. 5: 39). St. Croix is probably type locality of *P. laxum*, fide Hitchcock, Man. Grasses W.I. 215, 1936.

Paspalum paspalodes (Michx.) Scribn. (*Paspalum distichum* sensu auct. plur., non L., B. & W. 5: 41).

PENNISETUM Pers.

Pennisetum ciliare (L.) Link. — Teague Bay, *Frederiksen* 18-24 (FA).

SETARIA Beauv. (*Chaetochloa* Scribn.).

Setaria geniculata (Lam.) Beauv. (*Chaetochloa geniculata* (Lam.) Millsp. & Chase, B. & W. 5: 55).

*Setaria italica (L.) Beauv. (*Chaetochloa italica* (L.) Scribn., B. & W. 6: 332).

Setaria rariflora Milsan (*Chaetochloa rariflora* (Milsan) Hitchc. & Chase, B. & W. 5: 56).

Setaria setosa (Sw.) Beauv. (*Chaetochloa setosa* (Sw.) Scribn., B. & W. 5: 56).

*SORGHUM Moench (*Holcus* sensu B. & W. 5: 29, non L. sensu stricto).

*Sorghum bicolor Roxb. (*Holcus sorghum* L., B. & W. 5: 29).

SPARTINA Schreb.

Spartina patens (Ait.) Muhl. — Buck I. Børgesen in 1906 (US).

SPOROBOLUS R. Br.

*Sporobolus africanus (Poir.) Robyns & Tourn. (*Sporobolus berteroanus* (Trin.) Hitchc. & Chase, B. & W. 5: 64).

Sporobolus argutus (Nees) Kunth. — East End Point, *D. Smith* 18 (FA); *Fosberg* 54019 (US, FA). Hitchcock, Man. Grasses W.I., 84, regards this as a synonym of *S. pyramidatus* (Lam.) Hitchc.

Sporobolus tenuissimus (Schranck) O. Ktze. (*Sporobolus muralis* (Raddi) Hitchc. & Chase, B. & W. 5: 64). Fide Hitchcock, Man. Grasses W.I., 81.

TRAGUS Hall. (*Nazia* Adans.).

Tragus berteronianus Schult. (*Nazia aliena* sensu B. & W., non (Spreng.) Scribn., B. & W. 5: 31).

*TRICHOLAENA Schrad.

*Tricholaena rosea Nees. — Seen, well established, in 1972.

CYPERACEAE

CYPERUS L. (*Kyllinga* Rottb.).

*Cyperus alternifolius L. — Seen in 1969, planted.

Cyperus brevifolius (Rottb.) Hassk. (*Kyllinga brevifolia* Rottb., B. & W. 5: 79).

Cyperus flavus (Vahl) Nees (*Cyperus cayennensis* (Lam.) Britt., B. & W. 5: 86). Fide Alain, Rhodora 67: 320, 1965.

Cyperus nanus Willd. (*Cyperus granularis* (Desf.) Britt.). Fide Alain, Rhodora 67: 320, 1965 (B. & W. 5: 86).

Cyperus nanus var. subtenuis Kük. (*Cyperus tenuis* Sw.). Fide Alain, Rhodora 67: 320, 1965 (B. & W. 5: 87).

Cyperus obtusatus (Presl) Mattf. & Kük. (*Kyllinga pungens* Link). Fide Alain, Rhodora 67: 320, 1965 (B. & W. 5: 79).

Cyperus odoratus L., non sensu B. & W. (*Cyperus ferax* L. C. Rich. B. & W. 5: 89).

Cyperus planifolius L. C. Rich. (*Cyperus brunneus* Sw.). Fide Alain, Rhodora 67: 320, 1965 (B. & W. 5: 88).

Cyperus unifolius Boeckl. (*Cyperus filiformis* sensu B. & W. non Sw., B. & W. 5: 89).

ELEOCHARIS R. Br.

Eleocharis geniculata (L.) R. & S., non sensu B. & W. (*Eleocharis caribaea* (Rottb.) Blake, B. & W. 5: 91).

Eleocharis montana (HBK.) R. & S. (*Eleocharis nodulosa* (Roth) Schultes). Fide Alain, Rhodora 67: 320, 1965 (B. & W. 5: 92).

FIMBRISTYLIS Vahl.

Fimbristylis dichotoma L. (*Fimbristylis diphylla* (Retz.) Vahl, B. & W. 5: 95).

PALMAE (Arecaceae)

COCCOTHRINAX Sarg.

Coccothrinax barbadensis (Lodd. ex R. & S.) Becc., Webbia 2: 328, 1907. (*Thrinax barbadensis* Lodd. ex R. & S.; *Thrinax argentea* Lodd. ex Desf.; *Coccothrinax argentea* (Lodd. ex Desf.) Sarg. ex K. Schum.; *Coccothrinax eggersiana* Becc.; *Coccothrinax eggersiana* var. *sanctae-crucis* Becc.).

*PHOENIX L.

*Phoenix dactylifera L. — Seen planted in Christiansted, 1972.

*Phoenix roebelinii O'Brien. — Seen planted, in 1972.

*PRITCHARDIA Seem. & Wendl.

*Pritchardia pacifica Seem. & Wendl. — Seen planted, Teague Bay, 1972.

*Pritchardia thurstonii F. Muell. & Drude. — Seen planted in Cruzan Garden, 1972.

ROYSTONEA Cook.

Roystonea elata (Bartram) Harper (*Roystonea regia* (H.B.K.) Cook, B. & W. 5: 112; *Roystonea borinquena* Cook).

*VEITCHIA Wendl.

*Veitchia merrillii (Becc.) H. E. Moore (*Adonidia merrillii* Becc.).

*WASHINGTONIA Wendl. (*Neowashingtonia* Sudw.).

*Washingtonia filifera (Lind.) Wendl. (*Neowashingtonia filifera* (Lind.) Sudw., B. & W. 5: 119).

ARACEAE

ANTHURIUM Schott.

*Anthurium andraeanum Lindl. — Seen in gardens, 1972.

*CALADIUM Vent. (*Cyrtospadix* C. Koch).

*Caladium bicolor (Ait.) Vent. (*Cyrtospadix bicolor* (Ait.) B. & W., B. & W. 5: 126).

*DIEFFENBACHIA Schott.

*Dieffenbachia maculata (Lodd.) Bunt. — Teague Bay, W.I. Lab. *Hayes* 148 (FA).

*MONSTERA Schott.

*Monstera deliciosa Liebm. — Seen by Fosberg, 1972, cult.

*PHILODENDRON Schott.

*Philodendron selloum C. Koch. — Teague Bay, planted, *Hayes* 151 (FA).

*RHAPHIDOPHORA Hassk.

*Rhaphidophora aurea (Lind. & André) Birdsey (*Scindapsus aureus* Lind. & André). Seen planted in Christiansted, 1972.

*Rhaphidophora pinnata (L.) Schott. Seen planted in Christiansted, 1972.

BROMELIACEAE

TILLANDSIA L. (*Dendropogon* Raf.).

Tillandsia usneoides L. (*Dendropogon usneoides* (L.) Raf.). Eliza's Retreat, Jakobsberg, *Fosberg* 54153 (US, FA, FO). Seen also at Creque Dam.

COMMELINACEAE

CALLISIA L.

*Callisia fragrans (Lindl.) Woodson — Cotton Valley, Yellowcliff Bay, *Fosberg* 53937 (US, FA, FO).

COMMELINA L.

*Commelina diffusa Burm. f. (*Commelina longicaulis* Jacq., B. & W. 5: 145). Fide Alain, Rhodora 67: 323, 1965.

Commelina virginica L. (*Commelina elegans* H.B.K., B. & W. 5: 145). Fide Alain, Rhodora 67: 373, 1969.

*RHOEO Hance.

*Rhoeo spathacea (Sw.) Stearn (*Rhoeo discolor* (L'Hér.) Hance, B. & W. 5: 147).

*SETCREASIA K. Schum. & Syd.

*Setcreasia purpurea Boom — Teague Bay, planted, *Hayes* 136 (FA).

PONTEDERIACEAE

*EICHHORNIA Kunth (*Piaropus* Raf.).

*Eichhornia crassipes (Mart.) Solms (*Piaropus crassipes* (Mart.) Britt., B. & W. 5: 149).

LILIACEAE (sensu latissimo)

AGAVE L.

*Agave americana L. — Seen in gardens, 1972.

*ALOE L.

*Aloe barbadensis Mill. (*Aloe vera* L.; *Aloe vulgaris* Lam., B. & W. 5: 151).

*ASPARAGUS L.

*Asparagus plumosus Baker. — Seen, cultivated, 1972.

*Asparagus sprengeri Regel — Teague Bay, cultivated, *Hayes* 137 (FA).

*CHLOROPHYTUM Ker-Gawl.

*Chlorophytum comosum (Thurb.) Baker ? Seen in gardens, 1972.

*CORDYLINE R. Br., non sensu B. & W.

*Cordyline fruticosa (L.) Chev. Seen, planted, 1972.

*DRACAENA Vand.

*Dracaena fragrans (L.) Ker. — Seen, planted in Christiansted, 1972.

PANCRATIUM L.

Pancratium declinatum Jacq. (*Hymenocallis declinata* (Jacq.) M. Roem., B. & W. 5: 162). Fide Alain, Rhodora 67: 324, 1965.

*SANSEVIERIA Thunb. (*Cordyline* Adans., non R. Br.).

*Sansevieria hahnii Hort. — This diminutive bowstring hemp was seen cultivated, 1972.

*Sansevieria metallica Ger. & Labory (*Sansevieria guineensis* sensu B. & W. 5: 150, non (L.) Willd.). Differs most conspicuously from *S. trifasciata* in the lack of a conspicuous leaf appendage and slightly wider leaves with a narrow reddish stripe on margins. It is abundantly naturalized in a number of parts of the island. It is represented by good flowering material from Salt River, near Morningstar, *Fosberg* 54061 (US, FA).

*Sansevieria trifasciata Prain — This common cultivated species was seen around Christiansted as a pot plant. Its very erect leaves have terete appendages at their tips.

ZEPHYRANTHES Herb. (*Atamosco* Adans.).

Zephyranthes grandiflora Herb. (*Atamosco carinata* (Herb.) P. Wils., B. & W. 5: 159).

Zephyranthes puertoricensis Traub (*Atamosco tubispatha* sensu B. & W., non (L'Hér.) Maza, B. & W. 5: 158).

IRIDACEAE

ELEUTHERINE Herb. (*Galatea* Salisb.).

Eleutherine bulbosa (Mill.) Urb. (*Galatea bulbosa* (Mill) Britt., B. & W. 5: 166). Fide Alain, Rhodora 67: 324, 1965.

MUSACEAE

*MUSA L.

*Musa sapientum L. — Seen in gardens, 1972.

*RAVENALA L.

*Ravenala madagascariensis Gmel. Seen in gardens, 1972.

ZINGIBERACEAE

*ALPINIA L., non sensu B. & W.

*Alpinia purpurata (Viell.) K. Schum. — Seen, planted, Cruzan Garden and Christiansted, 1972.

RENEALMIA L. f. (*Alpinia* sensu B. & W., non L.).

Renealmia aromatica (Aubl.) Griseb. (*Alpinia aromatica* Aubl., B. & W. 5: 172).

*ZINGIBER Adans.

*Zingiber officinale Rosc. (*Zingiber zingiber* (L.) Karst., B. & W. 5: 173).

ORCHIDACEAE

EPIDENDRUM L. (*Anacheilium* Hoffmg.; *Auliza* Salisb.; *Encyclia* Hook.).

Epidendrum bifidum Aubl. (*Encyclia bifida* (Aubl.) B. & W.). Ridge above Cottongarden Pt., *D'Arcy* 4703 (FA).

Epidendrum brittonianum Hawkes (*Encyclia papilionacea* sensu B. & W. 5: 198, non (Vahl) Schltr.). Fide Alain, Rhodora 67: 326, 1965.

Epidendrum ciliare L. (*Auliza ciliaris* (L.) Salisb., B. & W. 5: 199). Fide Alain, Rhodora 67: 326, 1965.

Epidendrum cochleatum L. (*Anacheilium cochleatum* (L.) Hoffmg., B. & W. 5: 198). Fide Alain, Rhodora 67: 326, 1965.

SPIRANTHES Rich. (*Beadlea* Small).

Spiranthes elata (Sw.) L. C. Rich. (*Beadlea elata* (Sw.) Small, B. & W. 5: 187). Fide Alain, Rhodora 67: 325, 1965.

*VANILLA Mill.

*Vanilla mexicana Mill. — Seen in gardens, 1972.

PIPERACEAE

PIPER L. (*Pothomorphe* Miq.).

Piper peltatum L. (*Pothomorphe peltata* (L.) Miq., B. & W. 5: 229).

ULMACEAE

CELTIS L. (*Momisia* Dietr.).

Celtis iguanaea (Jacq.) Sarg. (*Momisia iguanaea* (Jacq.) Rose & Standl., B. & W. 5: 234).

MORACEAE

*ARTOCARPUS Forst.

*Artocarpus altilis (Park.) Fosb. (*Artocarpus communis* Forst., B. & W. 5: 241).

FICUS L.

Ficus citrifolia Mill. (*Ficus laevigata* Mill., B. & W. 5: 238).

*Ficus elastica Roxb. — Seen; small plants planted in some numbers, no large ones seen, 1972.

*Ficus lyrata Warb. — Seen; planted in Christiansted.

*Ficus microcarpa L. (*Ficus nitida* Thunb.; *Ficus retusa* sensu auct. plur., non L.). Seen in gardens, 1972.

Ficus obtusifolia H.B.K. (*Ficus urbaniana* Warb., B. & W. 5: 238; L. & W. 72).

Ficus trigonata L. (*Ficus crassinervia* Desf., B. & W. 5: 237).

URTICACEAE

LAPORTEA Gaud. (*Fleurya* Gaud.).

Laportea aestuans (L.) Chew (*Fleurya aestuans* (L.) Gaud., B. & W. 5: 245).

PROTEACEAE

*MACADAMIA F. Muell.

*Macadamia integrifolia Maiden & Betche. — Seen in garden, 1972.

POLYGONACEAE

*ANTIGONON Endl.

*Antigonon guatemalensis Meisn. (*Antigonon macrocarpum* Britt. & Small, B. & W. 5: 266). Fide Alain, Rhodora **67**: 328, 1965.

*Antigonon leptopus H. & A. — Near Two Friends, 400′, *D'Arcy* 4721 (FA). Common in cultivation and becoming naturalized locally.

COCCOLOBA L. (Conserved orthography. *Coccolobis* P. Br.).

Coccoloba diversifolia Jacq. (B. & W. 5: 267; L. & W. 76; *Coccolobis laurifolia* Jacq.). Fide Alain, Rhodora **67**: 329, 1965 (B. & W. 269).

Coccoloba microstachya Willd. (*Coccolobis obtusifolia* Jacq., B. & W. 5: 268). Fide Alain, Rhodora **67**: 329, 1965. Above W.I. Lab., Teague Bay, *D'Arcy* 4685 (FA); *Hayes* 105 (FA).

CHENOPODIACEAE

ATRIPLEX L.

Atriplex littoralis (Jacq.) Fawc. & Rendle (*Atriplex pentandra* (Jacq.) Standl., B. & W. 5: 272). Fide Alain, Rhodora **69**: 373, 1967.

AMARANTHACEAE

*ACHYRANTHES L., non sensu B. & W. (*Centrostachys* Wall. ex Roxb.).

*Achyranthes aspera L. (*Achyranthes indica* (L.) Mill.; *Centrostachys indica* (L.) Standl., B. & W. 5: 278). Belvedere Estate, *D'Arcy* 4711 (FA); Cathrine's Rest, on Granard Road, *Fosberg* 54102 (US, FA).

ALTERNANTHERA Forsk. (*Achyranthes* sensu B. & W., non L.).

Alternanthera paronychioides St. Hil. (*Alternanthera polygonoides* sensu B. & W., non (L.) R. Br., B. & W. 5: 279; 6: 344); *Achyranthes polygonoides* sensu B. & W., non (L.) Lam.). Fide Alain, Rhodora **67**: 329, 1965; Gooding et al., Fl. Barbados 138, 1965.

Alternanthera peploides (H. & B.) Urb. (*Achyranthes peploides* (H. & B.) Britt., B. & W. 5: 279).

Alternanthera portoricensis O. Ktze. (*Achyranthes portoricensis* (O. Ktze.) Standl., B. & W. 5: 280).

Alternanthera sessilis (L.) R. Br. ex DC. Canyon above Altona, 200′, *Fosberg* 54055 (US, FA).

AMARANTHUS L.

*Amaranthus viridis L., non sensu B. & W. (*Amaranthus gracilis* Desf., B. & W. 5: 277) Teague Bay, W.I. Lab., *Fosberg* 53986 (US, FA).

GOMPHRENA L.

Gomphrena decumbens Jacq. Teague Bay, *Hayes* 161 (FA).

NYCTAGINACEAE

BOERHAVIA L. (*Commicarpus* Standl.).

Boerhavia scandens L. (*Commicarpus scandens* (L.) Standl., B. & W. **6**: 345).

*BOUGAINVILLEA Comm. ex Juss.

*Bougainvillea glabra Choisy — Teague Bay, W.I. Lab., *Hayes* 145 (FA).

PORTULACACEAE

PORTULACA L.

Portulaca rubricaulis H.B.K. (*Portulaca phaeosperma* Urb., B. & W. 5: 300). Fide LeGrand, An. Mus. Hist. Nat. Montev. 7(3): 48-49, 1962.

NYMPHAEACEAE

NYMPHAEA L., non sensu B. & W. (*Castalia* Salisb.).

Nymphaea ampla (Salisb.) DC. (*Castalia ampla* Salisb., B. & W. 5: 304).

Nymphaea ampla var. pulchella (DC.) Casp. (*Castalia pulchella* (DC.) Britt., B. & W. 5: 304).

BASELLACEAE

ANREDERA Juss. (*Boussingaultia* H.B.K.).

Anredera leptostachys (Moq.) Steen. (*Boussingaultia leptostachys* Moq., B. & W. 5: 301). Fide Alain, Rhodora, 67: 330, 1965.

LAURACEAE

CINNAMOMUM Schaeff. (*Camphora* Fabr.; *Phoebe* Nees).

*Cinnamomum camphora (L.) Nees & Eberm. (*Camphora camphora* (L.) Karst., B. & W. 5: 324).

Cinnamomum elongatum (Vahl) Nees (B. & W. 5: 319). Fide Alain, Rhodora 67: 331, 1965.

*Cinnamomum verum Presl (*Cinnamomum zeylanicum* Bl., B. & W. 5: 324).

LICARIA Aubl. (*Acrodiclidium* Nees).

Licaria salicifolia (Sw.) Kost. (*Acrodiclidium salicifolium* (Sw.) Griseb., B. & W. 5: 317; L. & W. 112). Fide Alain, Rhodora 67: 330, 1965.

*PERSEA Mill.

*Persea americana Mill. (*Persea persea* (L.) Cocker., B. & W. 5: 318; L. & W. 128).

CRUCIFERAE (Brassicaceae)

*BRASSICA L.

*Brassica oleracea L. — Seen in garden, 1972.

*RORIPPA Scop. (*Nasturtium* R. Br. *Sisymbrium* sensu B. & W., non L.).

*Rorippa nasturtium-aquaticum (L.) Hayek (*Sisymbrium nasturtium-aquaticum* L., B. & W. 5: 329; *Nasturtium officinale* R. Br.).

*Rorippa portoricense (Spreng.) Stehlé — Wells Nursery, Fountain Valley, *Fosberg* 54070 (US). Locally common weed.

CAPPARIDACEAE

CLEOME L.

*Cleome viscosa L. (*Cleome icosandra* L., B. & W. 5: 331).

MORINGACEAE

*MORINGA Adans.

*Moringa oleifera Lam. (*Moringa moringa* (L.) Millsp., B. & W. 5: 337).

CRASSULACEAE

*KALANCHOE Adans. (*Bryophyllum* Salisb.).

*Kalanchoe pinnata (Lam.) Pers. (*Bryophyllum pinnatum* (Lam.) Kurz, B. & W. 5: 338).

*Kalanchoe tubiflora Hamet — Seen planted, 1972.

A number of other species of this genus are found in gardens or escaping.

ROSACEAE

*PRUNUS L. (*Amygdalus* L.).

*Prunus persica (L.) Batsch. (*Amygdalus persica* L.).

LEGUMINOSAE-MIMOSOIDEAE (Mimosaceae)

ACACIA Willd. (*Vachellia* W. & A.).

Acacia farnesiana (L.) Willd. (*Vachellia farnesiana* (L.) W. & A., B. & W. 5: 352).

CALLIANDRA Benth.

*Calliandra haematocephala Hassk. — Teague Bay, cultivated, *Multer* 36 (FA).

DESMANTHUS Willd. (*Acuan* Medic.).

Desmanthus depressus H. & B. (*Acuan depressum* (H. & B.) O. Ktze., B. & W. 5: 356).

Desmanthus virgatus (L.) Willd. (*Acuan virgatum* (L.) Medic., B. & W. 5: 356).

LEUCAENA Benth.

*Leucaena leucocephala (Lam.) deWit (*Leucaena glauca* sensu B. & W., non (L.) Benth., B. & W. 5: 355).

PROSOPIS L.

*Prosopis limensis Benth. Fide Alain. (Rhod. 67: 332).

LEGUMINOSAE-CAESALPINOIDEAE (Caesalpinaceae)

BAUHINIA L.

*Bauhinia blakeana Dunn. — Cruzan Garden, Calquhourn, *Baumwell* 7 (FA).

*Bauhinia coccinea DC. — Seen in gardens, 1972.

*Bauhinia variegata L. — Christiansted, *Baumwell* 1 (FA). Cultivated.

CAESALPINIA L. (*Guilandina* L.; *Poinciana* L.).

Caesalpinia bonduc (L.) Roxb. (*Guilandina crista* sensu B. & W., non L., B. & W. 5: 378). East of south of Westend Saltpond, west of Concordia, *Baumwell* 8 (FA).

Caesalpinia divergens Urb. (*Guilandina divergens* (Urb.) Britt., B. & W. 5: 379). East of south arm of Westend Saltpond, west of Concordia, *Baumwell* 9 (FA).

Caesalpinia melanosperma (Eggers) Urb. (*Guilandina melanosperma* Eggers, B. & W. 5: 380). North coast of East End east of Cramer Park, *Fosberg* 54063 (US, FA).

The last two are perhaps too close together, at least as to St. Croix specimens.

*Caesalpinia pulcherrima (L.) Sw. (*Poinciana pulcherrima* L., B. & W. 5: 376).

CASSIA L. (*Peiranisia* Raf.; *Herpetica* Raf.; *Senna* Mill.; *Adipera* Raf.; *Ditremexa* Raf.; *Emelista* Raf.; *Chamaecrista* Moench).

Cassia alata L. (*Herpetica alata* (L.) Raf., B. & W. 5: 374).

Cassia angustifolia Vahl (*Senna angustifolia* (Vahl) Batka, B. & W. 5: 373).

Cassia bicapsularis L. (*Adipera bicapsularis* (L.) B. & R., B. & W. 3: 370).

Cassia diffusa DC. (*Chamaecrista chamaecrista* sensu B. & W., non (L.) Britt., B. & W. 5: 367). Scenic Road, near Parasol Hill, 600 ft., *Baumwell* 4 (FA).

*Cassia fruticosa Mill. — Cruzan Garden, Calquhourn, *Baumwell* 2 (FA). Cultivated.

Cassia glandulosa var. swartzii (Wikstr.) Macbr. (*Cassia swartzii* Wikstr.; *Chamaecrista swartzii* (Wikstr.) Britt., B. & W. 5: 366).

*Cassia javanica L. (Fide Alain, Rhodora 67: 332). (*Cassia nodosa* Hamilt., B. & W. 5: 369). Seen in gardens, 1972.

Cassia obtusifolia L. (*Emilista tora* (L.) B. & R., B. & W. 5: 371).

Cassia occidentalis L. (*Ditremexa occidentalis* (L.) B. & R., B. & W. 5: 372).

Cassia polyphylla Jacq. (*Peiranisia polyphylla* (Jacq.) B. & R., B. & W. 5: 373).

Cassia portoricensis Urb. (*Chamaecrista portoricensis* (Urb.) Cook & Collins, B. & W. 5: 367). Scenic Road, near Parasol Hill, *Baumwell* 5 (FA).

LEGUMINOSAE-LOTOIDEAE (Fabaceae)

ABRUS L.

Abrus precatorius L. (*Abrus abrus* (L.) F. W. Wight, B. & W. 5: 411).

AESCHYNOMENE L.

Aeschynomene sensitiva Sw. East end of Airport, *Kaufman* 18 (FA).

ANDIRA Lam. (*Geoffrea* Wright).

Andira inermis H.B.K. (*Geoffrea inermis* (H.B.K.) Wright). Beck Grove, *Fosberg* 53954, 53954a (US, FA). Fruits eaten by bats. 53954a stones picked up under bat roost. Alain, Rhodora 69: 374, 1969 accepts the segregate genus, *Geoffrea* Wright.

*CAJANUS DC. (*Cajan* Adans.).

*Cajanus cajan (L.) Millsp. (*Cajan cajan* (L.) Millsp., B. & W. 5: 414).

CANAVALIA Adans. ex DC. (Conserved orthography. *Canavali* Adans.).

Canavalia rosea (Sw.) DC. (*Canavalia maritima* (Aubl.) Thou., B. & W. 5: 419).

CENTROSEMA Benth. (*Bradburya* Raf.).

Centrosema virginiana (L.) Benth. (*Bradburya virginiana* (L.) O. Ktze., B. & W. 5: 413).

CHRISTIA Moench (*Lourea* Neck. ex Desv.).

Christia vespertilionis (L. f.) Bakh. f. (*Lourea vespertilionis* (L.) Desv., B. & W. 5: 429).

DALBERGIA L. f. (*Ecastophyllum* Adans.).

Dalbergia ecastophyllum (L.) Taub. (*Ecastophyllum ecastophyllum* (L.) Britt., B. & W. 5: 406).

DESMODIUM Desv. (*Meibomia* Heist.; *Sagotia* Duch. & Walp.).

Desmodium axillare (Sw.) DC. (*Meibomia axillaris* (Sw.) O. Ktze., B. & W. 5: 402).

Desmodium canum (J. F. Gmel.) Schinz & Thell. (*Meibomia supina* (Sw.) Britt., B. & W. 5: 401). Bodkin Mill, 930′, *Fosberg* 54040 (US, FA).

Desmodium procumbens (Mill.) Hitchc. (*Meibomia procumbens* (Mill.) Hitchc., B. & W. 5: 404).

Desmodium tortuosum (Sw.) DC. (*Meibomia purpureum* (Mill.) Vail, B. & W. 5: 404).

Desmodium scorpiurus (Sw.) Desv. (*Meibomia scorpiurus* (Sw.) O. Ktze., B. & W. 5: 403).

Desmodium triflorum (L.) DC. (*Sagotia triflora* (L.) Duch. & Walp., B. & W. 5: 404).

PISCIDIA L. (*Ichthyomethia* P. Br.).

Piscidia piscipula (L.) Sarg. (*Ichthyomethia piscipula* (L.) Hitchc., B. & W. 5: 509).

RHYNCHOSIA Lour. (*Dolicholus* Medic.).

Rhynchosia minima (L.) DC. (*Dolicholus minimus* (L.) Medic., B. & W. 5: 416).

Rhynchosia reticulata (Sw.) DC. (*Dolicholus reticulatus* (Sw.) Millsp., B. & W. 5: 415).

SESBANIA Scop. (*Sesban* Adans.; *Agati* Adans.).

*Sesbania grandiflora (L.) Pers. (*Agati grandiflora* (L.) Desv., B. & W. 5: 396).

Sesbania sericea (Willd.) DC. (*Sesban sericea* (Willd.) DC., B. & W. 5: 395).

*Sesbania sesban (L.) Merr. (*Sesban sesban* (L.) Britt., B. & W. 5: 395).

STIZOLOBIUM P. Br.

Stizolobium pruriens (L.) Medic. (*Stizolobium pruritum* (Wight) Piper, B. & W. 5: 426). Fide Alain, Rhodora 65: 335, 1967.

TEPHROSIA Pers. (*Cracca* L.).

Tephrosia cinerea (L.) Pers. (*Cracca cinerea* (L.) Morong, B. & W. 5: 391).

VIGNA Savi

Vigna luteola (Jacq.) Benth. (*Vigna repens* (L.) O. Ktze., non Bak., B. & W. 5: 422).

OXALIDACEAE

OXALIS L. (*Ionoxalis* Small; *Xanthoxalis* Small).

Oxalis corniculata L. (*Xanthoxalis corniculata* (L.) Small, B. & W. 5: 431).

Oxalis corymbosa DC. (*Ionoxalis martiana* (Zucc.) Small).

Oxalis intermedia A. Rich. (*Ionoxalis intermedia* (A. Rich.) Small, B. & W. 5: 431).

ERYTHROXYLACEAE

ERYTHROXYLON L.

Erythroxylon rotundifolium Lunan (*Erythroxylon brevipes* DC., B. & W. 5: 433). Fide Alain, Rhodora 67: 335, 1965.

RUTACEAE

*CITRUS L.

*Citrus limon (L.) Burm. f. var. Rough, or Rough-skinned lemon. — Seen in gardens, 1972.

*Citrus nobilis Lour. — Seen in gardens, 1972.

*MURRAYA Koen. ex L. (*Chalcas* L.).

*Murraya paniculata (L.) Jack (*Murraya exotica* L.; *Chalcas exotica* (L.) Millsp., B. & W. 5: 545).

BURSERACEAE

BURSERA L. (*Elaphrium* Jacq.).

Bursera simaruba L. (*Elaphrium simaruba* (L.) Rose, B. & W. 5: 461).

MELIACEAE

*AZADIRACHTA A. Juss.

*Azadirachta indica A. Juss. — Seen in gardens, 1972.

*CHUKRASIA A. Juss.

*Chukrasia tabularis A. Juss. — Seen in gardens, 1972, introduced as a timber tree.

MALPIGHIACEAE

BYRSONIMA Rich.

Byrsonima coriacea var. spicata (Cav.) DC. (*Byrsonima spicata* Cav., B. & W. 5: 447).

Byrsonima lucida DC. — Sandy Point, s.w. of Westend Salt-pond, *Fosberg* 54086 (US, FA); *Frederiksen* 17-21 (FA); *Fosberg* 55361 (US, FA, FO).

GALPHIMIA Cav.

*Galphimia glauca Cav. (*Thryallis glauca* (Cav.) O. Ktze., B. & W. 5: 442).

HETEROPTERIS Kunth (*Banisteria* sensu B. & W., non L. as to St. Croix plants, acc. Alain, Rhodora 67: 335.)

Heteropteris laurifolia (L.) Juss. (*Banisteria laurifolia* L., B. & W. 5: 440).

Heteropteris purpurea (L.) Kunth (*Banisteria purpurea* L., B. & W. 5: 439).

MALPIGHIA L.

*Malpighia coccigera L. — Seen in gardens, 1972.

*Malpighia punicifolia L. — Seen in gardens, 1972.

STIGMAPHYLLON A. Juss.

Stigmaphyllon periplocifolium (Desf.) Juss. (*Stigmaphyllon lingulatum* (Poir.) Small, B. & W. 5: 441).

EUPHORBIACEAE

ADELIA L. (*Ricinella* M.-A.)

Adelia ricinella L. (*Ricinella ricinella* (L.) Brit., B. & W. 5: 488; *Ricinella pedunculosa* M.-A.)

*CODIAEUM A. Juss.

*Codiaeum variegatum (L.) Bl. — Seen commonly in gardens, 1972.

EUPHORBIA L. (*Aklema* Raf.; *Chamaesyce* S. F. Gray; *Dichylium* (Boiss.) Britt.; *Poinsettia* R. Grah.)

*Euphorbia antiquorum L. — Seen in gardens, 1972.

Euphorbia articulata Aubl. (*Chamaesyce articulata* (Aubl.) Britt., B. & W. 5: 505).

Euphorbia cyathophora Murr. (*Poinsettia cyathophora* (Murr.) Kl. & Gke., B. & W. 5: 498).

Euphorbia glomerifera (Millsp.) Wheeler (*Chamaesyce hypericifolia* sensu B. & W., non *Euphorbia hypericifolia* L., B. & W. 5: 501).

Euphorbia heterophylla L. (*Poinsettia heterophylla* (L.) Kl. & Gke., B. & W. 5: 498).

Euphorbia hirta L. (*Chamaesyce hirta* (L.) Millsp., B. & W. 5: 502).

Euphorbia hypericifolia L. (*Chamaesyce nutans* (Lag.) Small, B. & W. 5: 501).

*Euphorbia leucocephala Lotsy. — Seen in gardens, 1972.

Euphorbia mesembrianthemifolia Jacq. (*Euphorbia buxifolia* Lam.; *Chamaesyce buxifolia* (Lam.) Small, B. & W. 5: 504).

*Euphorbia milii Moul. (*Euphorbia splendens* Bojer.) Seen in gardens, 1972.

Euphorbia oerstedianum Kl. & Gke. (*Dychylium oerstedianum* (Kl. & Gke.) Britt., B. & W. 5: 499).

Euphorbia petiolaris Sims (*Aklema petiolare* (Sims) Millsp., B. & W. 5: 500).

*Euphorbia prostrata Ait. (*Chamaesyce prostrata* (Ait.) Small, B. & W. 5: 503).

*Euphorbia pulcherrima Willd. (*Poinsettia pulcherrima* (Willd.) R. Grah.) Seen in gardens, 1972.

Euphorbia serpens H.B.K. (*Chamaesyce serpens* (H.B.K.) Small, B. & W. 5: 502).

*Euphorbia thymifolia L. (*Chamaesyce thymifolia* (L.) Millsp., B. & W. 5: 503).

*Euphorbia tirucalli L. Seen in gardens, 1972.

JATROPHA L. (*Adenoropium* Pohl; *Curcas* Adans.).

*Jatropha curcas L. (*Curcas curcas* (L.) Britt. & Millsp., B. & W. 5: 484).

Jatropha gossypifolia L. (*Adenoropium gossypifolium* (L.) Pohl, B. & W. 5: 485).

*Jatropha intgerrima Jacq., Sel. Stirp. Amer. 256, *Pl.* 183, *f.* 74 [really 47 in plate], 1763. Seen in gardens, 1972.

***Jatropha integerrima** var. **hastata** (Jacq.) Fosberg, comb. nov. (*Jatropha hastata* Jacq., Sel. Stirp. Amer. 256, *Pl.* 173, *f.* 54, 1763.)

There seems no reason to disagree with McVaugh (Bull. Torr. Bot. Cl. 72: 274-275, 1945) that the group of *Jatropha* to which this plant belongs may best be regarded as composed of a single variable species, for which he chooses the name *J. integerrima* Jacq. However, some of the populations that have been given specific rank do really seem to exist, even though based principally on leaf characters. *Jatropha hastata* Jacq. characterized by broadly ovate-cordate, hastate leaves, is one such. It may well be that this distinctive population owes its numbers to vegetative horticultural multiplication. However, this only indicates a possible origin of the population, not its characteristics. Giving it varietal rank enables us to talk about it.

*Jatropha multifida L. (*Adenoropium multifidum* (L.) Pohl, B. & W. 5: 485).

*Jatropha podagrica Hook. — Seen in gardens.

*MANIHOT Adans.

*Manihot esculenta Crantz (*Manihot utilissima* Pohl; *Manihot manihot* (L.) Cocker., B. & W. 5: 493).

PHYLLANTHUS L. (*Cicca* L.)

*Phyllanthus acidus (L.) Skeels (*Cicca disticha* L., B. & W. 5: 475).

BUXACEAE

BUXUS L. (*Tricera* Sw.)

Buxus vahlii Baill. (*Tricera vahlii* (Baill.) Britt., B. & W. 5: 508).

ANACARDIACEAE

*SCHINUS L.

*Schinus terebinthifolius Raddi — Teague Bay, *Hayes* 135 (FA).

CELASTRACEAE

CASSINE L. (Elaeodendron Jacq.)

Cassine xylocarpa Vent. (*Elaeodendron xylocarpum* (Vent.) DC., B. & W. 5: 519).

CROSSOPETALUM P. Br. (*Rhacoma* L.)

Crossopetalum rhacoma Crantz (*Rhacoma crossopetalum* L., B. & W. 5: 517).

SAPINDACEAE

CARDIOSPERMUM L.

Cardiospermum halicacabum var. microcarpum (H.B.K.) Bl. (*Cardiospermum microcarpum* H.B.K., B. & W. 5: 525).

RHAMNACEAE

COLUBRINA Rich.

Colubrina arborescens (Mill.) Sarg. (*Colubrina colubrina* (Jacq.) Millsp., B. & W. 5: 536).

ZIZYPHUS Mill. (*Sarcomphalus* P. Br.)

*Zizyphus mauritiana Lam. — Seen commonly on roadsides, 1972.

Zizyphus reticulata Vahl (*Sarcomphalus reticulatus* (Vahl) Urb., B. & W. 5: 534).

TILIACEAE

TRIUMFETTA L.

Triumfetta rhomboidea Jacq. (*Triumfetta bartramia* (L.) L., B. & W. 5: 544; *Triumfetta excisa* Urb., B. & W. 5: 544).

MALVACEAE

ABUTILON Mill.

Abutilon americanum (L.) Sweet (*Abutilon abutiloides* (Jacq.) Garcke, B. & W. 5: 547).

*GOSSYPIUM L.

*Gossypium arboreum var. nadam (Watt) Prokh. (*Gossypium barbadense* sensu B. & W. 5: 567, non L.). Fide Alain, Rhod. 67: 340, 1065.

*Gossypium hirsutum L. — Christiansted, *Fosberg* 53936 (US, FA).

HIBISCUS L. (*Abelmoschus* Medic.; *Pariti* Adans.)

*Hibiscus esculentus L. (*Abelmoschus esculentus* (L.) Moench, B. & W. 5: 564). Seen in gardens, 1972.

*Hibiscus schizopetalus L. — Seen in gardens, 1972.

Hibiscus tiliaceus L. (*Pariti tiliaceum* (L.) St. Hil., B. & W. 5: 567).

MALVASTRUM A. Gray

Malvastrum americanum (L.) Torr. (*Malvastrum spicatum* (L.) A. Gray, B. & W. 5: 550).

PAVONIA Car. (*Malache* Vogel).

Pavonia scabra (Vogel) Ciferri (*Malache scabra* Vogel, B. & W. 5: 560).

SIDA L.

Sida acuta Burm. f. (*Sida carpinifolia* L. f.).

Sida pyramidata Desf. Teague Bay, *Fosberg* 53982 (US, FA).

Sida salviaefolia Presl (*Sida erecta* Macf.).

STERCULIACEAE

AYENIA L.

Ayenia insularis Crist. (*Ayenia pusilla* sensu B. & W., non L., B. & W. 5: 574).

*BRACHYCHITON Schott & Endl. (*Sterculia* L. p.p., sensu B. & W.).

*Brachychiton populneum R. Br. (*Sterculia diversifolia* G. Don, B. & W. 5: 576).

GUAZUMA Adans.

Guazuma ulmifolia Lam. (*Guazuma guazuma* (L.) Cocker., B. & W. 5: 575).

MELOCHIA L. (*Moluchia* Medic.).

Melochia pyramidata L. (*Moluchia pyramidata* (L.) Britt., B. & W. 5: 572). Fide Goldberg, Contr. U.S.N.H. 34: 337-341, 1967.

Melochia tomentosa L. (*Moluchia tomentosa* (L.) Britt., B. & W. 5: 571). Goldberg, Contr. U.S.N.H. 34: 327-373, 1967, admits two varieties of this species, var. *tomentosa* and var. *frutescens* (Jacq.) DC., from St. Croix, but the characters by which they are separated are not convincing and, at least in St. Croix, field observations do not suggest two genetically distinct populations.

WALTHERIA L.

Waltheria indica var. americana (L.) R. Br. ex Hosaka (*Waltheria americana* L., B. & W. 5: 573).

GUTTIFERAE (Clusiaceae)

CALOPHYLLUM L.

Calophyllum calaba L. (*Calophyllum brasiliense* var. *antillanum* (Britt.) Standl., L. & W. 352; *Calophyllum antillanum* Britt., B. & W. 5: 584; Synonymy acc. Howard, Jour. Arn. Arb. 43: 397-8, 1963).

FLACOURTIACEAE

XYLOSMA Forst. f. (*Myroxylon* Forst.).

Xylosma buxifolia A. Gray (*Myroxylon buxifolium* (A. Gray) Kr. & Urb., B. & W. 5: 593).

PASSIFLORACEAE

PASSIFLORA L.

Passiflora foetida var. hispida (DC.) Killip — Belvedere Estate, *D'Arcy* 4740 (FA).

Passiflora suberosa L. (*Passiflora pallida* L., B. & W. 5: 602).

CUCURBITACEAE

*CUCUMIS L.

*Cucumis sativus L. — Seen in gardens.

*CUCURBITA L. (*Pepo* Mill.).

*Cucurbita ficifolia Bouché (*Pepo ficifolia* (Bouché) Britt., B. & W. 6: 266).

*Cucurbita moschata (Duch.) Duch. & Pou. (*Pepo moschata* (Duch.) Britt., B. & W. 6: 265).

*LAGENARIA Ser. (*Cucurbita* sensu B. & W., non L.).

*Lagenaria siceraria (Mol.) Standl. (*Cucurbita lagenaria* L., B. & W. 6: 262).

CACTACEAE

CEREUS Mill. (*Acanthocereus* B. & R.; *Hylocereus* B. & R.; *Selenicereus* B. & R.).

Cereus grandiflorus (L.) Mill. (*Selenicereus grandiflorus* (L.) B. & R., B. & W. 5: 616).

Cereus pentagonus (L.) Harv. (*Acanthocereus pentagonus* (L.) B. & R., B. & W. 5: 614).

Cereus pteranthus L. & O. (*Selinicereus pteranthus* (L. & O.) B. & R., B. & W. 5: 616).

Cereus trigonus Haw. (*Hylocereus trigonus* (Haw.) Saff., B. & W. 5: 615).

Cereus undatus Haw. (*Hylocereus undatus* (Haw.) B. & R., B. & W. 5: 615).

MELOCACTUS Link & Otto (*Cactus* L. p.p. sensu B. & W.).

Melocactus intortus (Mill.) Urb. (*Cactus intortus* Mill.).

*PERESKIA Mill.

*Pereskia aculeata Mill. (*Pereskia pereskia* (L.) Karst., B. & W. 5: 608).

LYTHRACEAE

*LAGERSTROEMIA L.

*Lagerstroemia indica L. — Seen in gardens, 1972.

COMBRETACEAE (Terminaliaceae)

*QUISQUALIS L.

*Quisqualis indica L. — Seen in gardens, 1972.

LECYTHIDACEAE

*BARRINGTONIA Forst.

*Barringtonia asiatica (L.) Kurz. Seen in 1972, planted.

MYRTACEAE

EUGENIA L. (*Jambos* Adans.).

*Eugenia jambos L. (*Jambos jambos* (L.) Millsp., B. & W. **6**: 41).

*Eugenia malaccensis L. (*Jambos malaccensis* (L.) DC., B. & W., **6**: 41).

PIMENTA Lindl. (*Amomis* Berg.).

*Pimenta dioica (L.) Merr. (*Pimenta pimenta* (L.) Cocker., B. & W. **6**: 42).

Pimenta racemosa (Mill.) J. W. Moore (*Caryophyllus racemosa* Mill.; *Amomis caryophyllata* (Jacq.) Krug. & Urb., B. & W. **6**: 27; *Pimenta acris* (Sw.) Kostel.).

PSIDIUM L.

*Psidium cattleianum Sabine — Seen in gardens, 1972.

ONAGRACEAE

LUDWIGIA L. (*Jussiaea* L.).

Ludwigia erecta (L.) Hara (*Jussiaea erecta* L., B. & W. **6**: 46).

Ludwigia octovalvis (Jacq.) Raven (*Jussiaea angustifolia* sensu B. & W., non Lam., B. & W. **6**: 46).

ARALIACEAE

*POLYSCIAS Forst.

*Polyscias fruticosa (L.) Harms — Seen in gardens, 1972.

*Polyscias guilfoylei (Bull) Bailey — Seen in gardens, 1972.

*Polyscias tricochleata (Mig.) Fosb. Seen in gardens, 1972.

*SCHEFFLERA Forst.

*Schefflera actinophylla (Endl.) Harms (*Brassaia actinophylla* Endl.). Teague Bay, W.I. Lab., *Multer* 56 (FA).

THEOPHRASTACEAE

JACQUINIA L.

Jacquinia arborea Vahl (*Jacquinia barbasco* sensu B. & W., non (Loefl.) Mez., B. & W. **6**: 62). Salt River Inlet. *D'Arcy* 4722 (FA).

MYRSINACEAE

ARDISIA Sw. (*Icacorea* Aubl.).

Ardisia obovata Desv. (*Icacorea guadalupensis* (Duch.) Britt., B. & W. **6**: 57).

PLUMBAGINACEAE

PLUMBAGO L.

*Plumbago auriculata Lam. (*Plumbago capensis* Thunb.). Teague Bay, *Multer* 55 (FA).

*Plumbago indica L. — Seen in garden, 1972.

Plumbago zeylanica L. — Reported by West fide B. & W. **6**: 63. This is an Indo-Pacific species similar to *P. scandens* L. The St. Croix record is doubtless based upon a misidentification of material of *P. scandens* and should be deleted from the St. Croix flora.

SAPOTACEAE

MANILKARA Adans. (*Achras* L.).

Manilkara zapota (L.) v. Royen (*Achras zapota* L., B. & W. **6**: 67).

POUTERIA Aubl.

Pouteria multiflora (A. DC.) Baehni (*Lucuma multiflora* A. DC., B. & W. **6**: 67).

OLEACEAE

JASMINUM L.

*Jasminum fluminense Vell. Naturalized in canyon on

north slope, Altona-Longford Road, about 110 m. *Fosberg* 54044 (US, FO, FA).

*Jasminum multiflorum (Burm. f.) Andr. (*Jasminum pubescens* (Retz.) Willd., B. & W. 6: 80).

APOCYNACEAE

*ADENIUM R. & S.

*Adenium coetaneum Stapf. Seen in gardens, 1972.

*ALLAMANDA L.

*Allamanda hendersonii Bull. — Seen in gardens, 1972.

*CARISSA L.

*Carissa macrocarpa (Eckl.) A. DC. Seen in gardens, 1972.

*NERIUM L.

*Nerium oleander L. — Seen in gardens; O. & B. 76-78.

*Nerium oleander var. indicum (Mill.) Deg. & Greenw. (*Nerium indicum* Mill.). Seen in gardens, 1972.

PLUMERIA L. (*Plumiera* L., orthographic variant. B. & W. 1: 87).

PRESTONIA P. Br.

Prestonia agglutinata (Jacq.) Woods. (*Echites agglutinata* Jacq., B. & W. 6: 92).

RAUVOLFIA L.

Rauvolfia nitida Jacq. (*Rauvolfia tetraphylla* sensu B. & W., non L., B. & W. 6: 90).

TABERNAEMONTANA L.

*Tabernaemontana divaricata (L.) R. Br. (*Tabernaemontana coronaria* Willd.; *Ervatamia divaricata* (L.) Burk.). Seen in gardens.

*THEVETIA Juss. ex Endl. (*Cerbera* sensu B. & W., non L.).

*Thevetia peruviana (L.) Pers. (*Cerbera thevetia* L., B. & W. 6: 91).

ASCLEPIADACEAE

*CRYPTOSTEGIA R. Br.

*Cryptostegia grandiflora (Roxb.) R. Br. — Seen in gardens; O. & B. 38-39.

CYNANCHUM L. (*Metastelma* R. Br.).

Cynanchum grisebachianum (Schltr.) Alain (*Metastelma decaisneanum* Schltr., B. & W. 6: 98).

Cynanchum parviflorum Sw. (*Metastelma parviflora* R. Br., B. & W. 6: 97).

MATELEA Aubl. (*Ibatia* Decne.).

Matelea maritima (Jacq.) Woods. (*Ibatia maritima* (Jacq.) Decne., B. & W. 6: 99).

SARCOSTEMMA R. Br. (*Funastrum* Fourn.).

Sarcostemma clausum (Jacq.) R. & S. (*Funastrum clausum* (Jacq.) Schltr., B. & W. 6: 99).

*STEPHANOTIS Thou.

*Stephanotis floribunda Brongn. — Seen in gardens, 1972.

CONVOLVULACEAE (Incl. Cuscutaceae)

EVOLVULUS L.

Evolvulus alsinoides var. linifolius (L.) Bak. (*Evolvulus linifolius* L., B. & W. 6: 105).

IPOMOEA L. (*Calonyction* Choisy; *Exogonium* Choisy; *Quamoclit* Moench).

Ipomoea alba L. (*Calonyction aculeatum* (L.) House, B. & W. 6: 107).

Ipomoea fistulosa Mart. ex Choisy. — Teague Bay, The Reef, *D. Smith* 16 (FA).

Ipomoea hederifolia L. (*Quamoclit coccinea* sensu B. & W., non (L.) Moench, B. & W. 6: 109).

Ipomoea macrantha R. & S. (*Calonyction tuba* (Schlecht.) Colla, B. & W. 6: 108; *Ipomoea tuba* (Schlecht.) G. Don).

Ipomoea pes-caprae subsp. brasiliensis (L.) v. Ooststr. (*Ipomoea pes-caprae* sensu B. & W. 6: 113, non *Ipomoea pes-caprae* (L.) L. var. *pes-caprae*).

Ipomoea quamoclit L. (*Quamoclit quamoclit* (L.) Britt., B. & W. 6: 108).

Ipomoea solanifolia L. (*Exogonium solanifolium* (L.) Britt., B. & W. 6: 109).

Ipomoea steudelii Millsp. (*Exogonium arenarium* Choisy; *Ipomoea arenaria* (Choisy) Steud., non R. & S., B. & W. 6: 110).

Ipomoea violacea L. (*Ipomoea tricolor* Cav., B. & W. 6: 47).

JACQUEMONTIA Choisy (*Thyella* Raf.).

Jacquemontia cumanensis var. — East Point, *Fosberg* 54016 (US, FA).

Jacquemontia tamnifolia (L.) Griseb. (*Thyella tamnifolia* Raf., B. & W. 6: 107).

MERREMIA Dennst.

Merremia aegyptia (L.) Urb. (*Ipomoea aegyptia* L., B. & W. 6: 112).

Merremia quinquefolia (L.) Hall. f. (*Ipomoea quinquefolia* L., B. & W. 6: 114).

Merremia tuberosa (L.) Rendle (*Operculina tuberosa* (L.) Meissn., B. & W. 6: 118).

Merremia umbellata (L.) Hall. f. (*Ipomoea polyanthes* R. & S.).

STICTOCARDIA Hall. f.

Stictocardia campanulata (L.) Merr. (*Rivea campanulata* (L.) House).

HYDROPHYLLACEAE

NAMA L. (*Marilaunidium* O. Ktze.).

Nama jamaicensis L. (*Marilaunidium jamaicense* (L.) O. Ktze.).

BORAGINACEAE (Incl. Ehretiaceae)

CORDIA L. (*Calyptrocordia* Britt.; *Cerdana* R. & P.; *Varronia* P. Br.).

Varronia may be a distinct genus, judging by palynological evidence (Nowicke, pers. comm.) but until its morpho-

logical characters are more clearly set forth we will regard it as a well marked section of *Cordia.*

Cordia alliodora (R. & P.) Oken (*Cerdana alliodora* R. & P., B. & W. **6**: 123).

Cordia dentata Poir. (*Calyptrocordia alba* sensu B. & W. **6**: 123, non *Cordia alba* (Jacq.) R. & S.).

Cordia globosa (Jacq.) H.B.K. (*Varronia globosa* Jacq., B. & W. **6**: 127).

Cordia polycephala (Lam.) Johnst. (*Varronia corymbosa* (L.) Desv., B. & W. **6**: 127).

Cordia rickseckeri Millsp. East End, North Coast, *Fosberg* 54062 (US).

*Cordia sebestena L. — Seen in gardens, 1972.

Cordia stenophylla Alain (*Varronia angustifolia* West, B. & W. **6**: 126).

HELIOTROPIUM L. (*Schobera* Scop.; *Tiaridium* Lehm.).

Heliotropium angiospermum Mun. (*Schobera angiosperma* (Mun.) Britt., B. & W. **6**: 135).

Heliotropium indicum L. (*Tiaridium indicum* (L.) Lehm., B. & W. **6**: 134).

TOURNEFORTIA L. (*Mallotonia* Britt.).

Tournefortia gnaphalodes L. (*Mallotonia gnaphalodes* (L.) Britt., B. & W. **6**: 131).

Tournefortia volubilis L. (*Tournefortia microphylla* Bert., B. & W. **6**: 134).

VERBENACEAE

AVICENNIA L.

Avicennia germinans (L.) L. (*Avicennia nitida* Jacq.).

CLERODENDRUM L. (*Siphonanthus* L.; *Volkameria* L.; *Clerodendron* L.).

Clerodendrum aculeatum (L.) Schlecht. (*Volkameria aculeata* L., B. & W. **6**: 150).

Clerodendrum indicum (L.) O. Ktze. (*Siphonanthus indicus* L., B. & W. **6**: 151).

Clerodendrum inerme (L.) Gaertn. Fide Alain, Rhodora 67: 350, 1965, but rather unlikely in St. Croix.

LANTANA L.

Lantana arida Britt. — Fide Alain, Rhodora 67: 349, 1965.

Lantana camara var. aculeata (L.) Mold. (*Lantana aculeata* L., B. & W. 6: 140).

Lantana insularis Mold. — Fide Alain, Rhodora 67: 349, 1965.

Lantana involucrata f. **candida** Fosb. n. f. *Ab var. involucrata floribus albis differt.* Flowers white, rather than light purple. St. Croix; east of South arm of Westend Saltpond, west of Concordia, on sand flats, *Fosberg* 54079 (US, type, FA).

Lantana involucrata var. odorata (L.) Mold. — Fide Alain, Rhodora 67: 349, 1965.

LIPPIA L. (*Phyla* Lour.).

Lippia nodiflora var. reptans (H.B.K.) O. Ktze. (*Lippia reptans* H.B.K.; *Phyla nodiflora* var. *reptans* (H.B.K.) Mold.).

Lippia strigulosa Mart. & Gal. f. **parvifolia** (Mold.) Fosberg, new comb. (*Phyla yucatana* var. *parvifolia* Moldenke, Phytologia 2: 141, 1946; *Phyla strigulosa* var. *parvifolia* (Mold.) Mold., Phytologia 2: 233, 1947; *Phyla strigulosa* f. *parvifolia* (Mold.) Mold. ex Alain, Rhodora 67: 349, 1965; Fide Alain, l.c., sub *Phyla*).

*PETRAEA L.

*Petraea volubilis L. — Seen in gardens, 1972.

STACHYTARPHETA Vahl (*Valerianoides* Medic.).

Stachytarpheta jamaicensis (L.) Vahl (*Valerianoides jamaicensis* (L.) O. Ktze., B. & W. 6: 144).

VERBENA L.

*Verbena tenuisecta Briq. ? Seen in garden, 1972.

VITEX L.

Vitex negundo var. intermedia (P'ei) Mold. — Fide Alain, Rhodora 67: 349, 1965.

ACANTHACEAE

*ASYSTASIA Bl.

*Asystasia gangetica (L.) T. Anders. — Seen in gardens, 1972.

BLECHUM P. Br.

Blechum brownei Juss. (*Blechum blechum* (L.) Millsp., B. & W. **6**: 210).

*CROSSANDRA Salisb.

*Crossandra infundibuliformis (L.) Nees. — Seen in gardens, 1972.

DICLIPTERA Juss. (*Diapedium* Konig.).

Dicliptera assurgens (L.) Juss. (*Diapedium assurgens* (L.) O. Ktze., B. & W. **6**: 215).

*GRAPTOPHYLLUM Nees

*Graptophyllum pictum (L.) Griff. — Seen in gardens, 1972.

JUSTICIA L. (*Stethoma* Raf.).

Justicia pectoralis Jacq. (*Stethoma pectoralis* (Jacq.) Raf., B. & W. **6**: 218).

*PSEUDERANTHEMUM Radlk.

*Pseuderanthemum carruthersii (Seem.) Guill. — Seen in gardens, 1972.

*THUNBERGIA Retz.

*Thunbergia grandiflora Roxb. — Seen in gardens, 1972.

RUBIACEAE

HAMELIA Jacq.

Hamelia patens Jacq. (*Hamelia erecta* Jacq., B. & W. **6**: 233).

HEDYOTIS L. (*Oldenlandia* L.).

Hedyotis callitrichoides (Griseb.) Lewis. (*Oldenlandia callitrichoides* Griseb., B. & W. **6**: 225). This delicate creeping species still persists in moist crevices in pavement and sidewalks in Christiansted, *Fosberg* 53932 (US, FA).

Hedyotis corymbosa (L.) Lam. (*Oldenlandia corymbosa* L. B. & W. **6**: 224).

*IXORA L.

*Ixora casei Hance. — Seen in gardens, 1972.

*Ixora coccinea L. — Teague Bay, W.I. Lab., *Hayes* 136 (FA).

*PENTAS Benth.

*Pentas lanceolata (Forsk.) K. Schum. — Seen in gardens, 1972.

PSYCHOTRIA L.

Psychotria microdon (DC.) Urb. (*Psychotria pinularis* Sessé & Moç., B. & W. **6**: 245).

Psychotria pubescens Sw. — "The Rain Forest" between Est. Prosperity and Est. North Star, *Fosberg* 54069 (US, FA).

RANDIA L.

Randia aculeata L. (*Randia mitis* L., B. & W. **6**: 231).

SPERMACOCE L. (*Borreria* Mey.).

Spermacoce confusa Rendle (*Spermacoce tenuior* sensu B. & W. **6**: 256, non L.).

*Spermacoce ocymoides Burm. f. (*Borreria ocimoides* (Burm. f.) DC., B. & W. **6**: 255).

Spermacoce suffrutescens Jacq. (*Borreria laevis* sensu B. & W. **6**: 255, non *Spermacoce laevis* Lam.).

Spermacoce tenuior L. (*Spermacoce riparia* C. & S.).

Spermacoce verticillata L. (*Borreria verticillata* (L.) Mey., B. & W. 2: 256).

STRUMPFIA Jacq.

Strumpfia maritima Jacq. — Setting Point, *D'Arcy* 4826 (FA).

CAMPANULACEAE (Incl. Lobeliaceae)

HIPPOBROMA G. Don (*Isotoma* sensu B. & W.).

Hippobroma longiflora (L.) G. Don (*Isotoma longiflora* (L.) Presl, B. & W. **6**: 273).

GOODENIACEAE

SCAEVOLA L.

*Scaevola taccada (Gaertn.) Roxb. — Many young plants seen in pots in Wells Nursery, Fountain Valley.

COMPOSITAE

(Incl. Asteraceae, Cichoriaceae, Ambrosiaceae)

BIDENS L. (*Cosmos* Cav.).

Bidens caudata (H.B.K.) Sch.-Bip. (*Cosmos caudatus* H.B.K. B. & W. **6**: 314).

CONYZA L.

Conyza apurensis H.B.K. (*Leptilon chinensis* (Jacq.) Britt. B. & W. **6**: 296).

ECLIPTA L. *Verbesina* sensu B. & W., non L.).

Eclipta alba (L.) Hassk. (*Verbesina alba* L., B. & W. **6**: 303).

ELEPHANTOPUS L.

Elephantopus mollis H.B.K. (*Elephantopus scaber* sensu Alain, Rhodora **67**: 354, 1965, non L.).

*EMILIA Cass.

*Emilia fosbergerii Nicolson — Mt. Pleasant, Scenic Rd., 500 ft., *Forbes* 48 (FA); between Annaly and Bodkin, 650 ft., *Fosberg* 55326 (US, FA, FO).

EUPATORIUM L. (sensu lato) (*Osmia* Sch.-Bip.; *Hebeclinum* DC.).

Eupatorium corymbosum Aubl. (*Osmia corymbosa* (Aubl.) B. & W., B. & W. **6**: 288).

Eupatorium macrophyllum L. *Hebeclinum macrophyllum* (L.) DC., B. & W. **6**: 287).

Eupatorium odoratum L. (*Osmia odorata* (L.) Sch.-Bip., B. & W. **6**: 287).

Eupatorium sinuatum Lam. (*Osmia sinuata* (Lam.) Britt., B. & W. **6**: 288).

*GYNURA Cass.

*Gynura aurantiaca DC. Seen in gardens, 1970.

LACTUCA L. (*Brachyramphus* DC.).

Lactuca intybacea Jacq. (*Brachyramphus intybaceus* (Jacq.) DC., B. & W. 6: 276).

*Lactuca sativa L. Seen in gardens, 1972.

*LAGASCEA Cav. (*Nocca* Cav.).

*Lagascea mollis Cav. (*Nocca mollis* (Cav.) Jacq.). Corn Hill, *Fosberg* 54106 (US, FO, FA); East of Alexander Hamilton Airport, *Fosberg* 54120 (US, FA); Teague Bay, West Indies Lab., *Fosberg* 54141 (US, FA, FO).

PLUCHEA Cass.

Pluchea carolinensis (Jacq.) D. Don (*Pluchea odorata* (L.) Cass., B. & W. 6: 298).

SENECIO L.

*Senecio confusus Britt. N. n. w. Cathrine's Rest, *Fosberg* 54119 (US, FA).

XANTHIUM L.

Xanthium strumarium L. (*Xanthium chinense* Mill., B. & W. 6: 278).

*YOUNGIA Cass.

*Youngia japonica (L.) DC. (*Crepis japonica* L.). Fountain Valley, abundantly naturalized around old nursery, *Fosberg* 54074 (US, FA).

BOTANY DEPARTMENT
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STUDIES ON NEW ENGLAND AGARICS, I.

Howard E. Bigelow

In the following contribution, one species in *Collybia*, *C. compressiceps*, and two in *Mycena*, *M. macilenta* and *M. madorophila*, are described as new to science. The proper generic status for *Clitocybe marginata* Peck also has been determined, resulting in the proposal of a new combination, *Callistosporium marginatum*. An interesting and uncommon *Amanita* of hardwoods, *A. spreta* of Peck, is described from Massachusetts specimens.

The colors noted in the descriptions are those of Ridgway (1912).

Amanita spreta (Peck) Saccardo, Syll. Fung. 5: 12. 1887. *Fig. 1*.

Agaricus spretus Peck, New York State Mus. Rep. **32**: 24. 1879.

Pileus 3-11 cm broad, obtuse conic with incurved margin at first, becoming broadly convex and finally plane, margin sometimes elevated in age, striate, slightly umbonate at times in large expanded caps, surface subviscid but soon dry, dull, glabrous and smooth, innately fibrillose in places and ± radiate toward margin, dark gray brown to umbrinous young, becoming pale gray brown in age, disc usually remaining dark, extreme margin pallid at times; context thin, soft but brittle, white. Odor none.

Lamellae free or slightly adnexed, close, medium broad (up to 12 mm), tapered at ends, white, edges crenate under a lens.

Stipe 7-17 cm long, apex (4-)10-15 mm thick, equal or tapering upward, base up to 2.5 cm thick, sheathed by distinct volva, curved near base at times, stuffed, pruinose to furfuraceous above annulus, scabrous to innately fibrillose below, white but becoming dingy on bruising.

Fig. 1. *Amanita spreta* (Peck) Saccardo × 1.

Annulus white but grayish or brownish in age, membranous but fragile, flared, soon pendant, only slightly striate on top, fibrillose and dull on both surfaces, superior.

Volva white, cuplike, even or more often split at top 1-3 times, somewhat flared, up to 3.5 cm long.

Spores (9-)10-12(-13) × 6.5-8 μm, elliptic, smooth, not amyloid, deposit white. Basidia 33-45 × 8-10 μm, 4-spored, hymenium pale dingy yellowish in mass in KOH. Pileus surface hyaline in KOH, consisting of a layer of hyphae which gelatinize, ± cylindric but usually curled and flexuous, subsurface layer brownish in KOH, pigment intracellular, hyphae cylindric, 2-6(-8) μm diam.; context of cylindric or broad cylindric hyphae, 3-13 μm diam., rarely with oleiferous hyphae, clamp connections present. Hymenophoral trama parallel or slightly divergent in unexpanded specimens, undulate-subparallel in old specimens, hyphae cylindric, 2-8 μm diam., or somewhat inflated, up to 20 μm diam. Annulus consisting of a mixture of sphaerocysts and hyphae, hyphae cylindric, 2-3.5(-9) μm diam., sphaerocysts 10-45 μm diam., walls thin, clamp connections present. Volva mostly of cylindric hyphae, 2.5-10 μm diam., clamp connections large and abundant, walls slightly thickened at times, occasional oleiferous hyphae, occasional ellipsoid cells, 27-52 μm diam.

Single or scattered. In grassy and herbaceous open area, scattered hardwoods of beech and oak. August.

Material examined. **Massachusetts:** *Bigelow* 14723, 15797, 15805 (MASS).

In my experience, this species does not appear to be common in New England; also, there are relatively few reports in the literature. Pomerleau (1966) has noted fruitings in adjacent Quebec, and of course Peck's first specimens were found in New York State.

The distinct sheathing and free-margined volva of *Amanita spreta* separates it easily in the field from most Amanitas which have similar colors to the pileus (e.g., *A. brunnescens, A. pantherina, A. excelsa*). However, *A. phalloides* has the same volval type as *A. spreta,* and the

pileus can fade to an umbrinous color like that of *A. spreta.* Conceivably, the two species could then be difficult to distinguish. Microscopic characters of course are distinctive — *A. phalloides* has amyloid, globose to subglobose spores and no clamp connections on hyphae of the basidiocarp. Thus far, I know of no collections of the true *A. phalloides* in New England, but its presence is quite possible in view of the reports by Tanghe and Simons (1973) of fruitings in New York, New Jersey and Pennsylvania.

Callistosporium marginatum (Peck) Bigelow, comb. nov.
Basionym: *Clitocybe marginata* Peck, Bull. Torrey Bot. Club 29: 558. 1902.
Monadelphus marginatus (Peck) Murrill, Mycologia 7: 282. 1915.

"Pileus fleshy, rather thick, subcampanulate, becoming convex, obtuse or broadly umbonate, glabrous or nearly so, dry, bay red verging to mahogany color, the margin at first involute, flesh yellow; lamellae narrow, close, decurrent, yellowish, reddish on the edge; stem nearly equal, stout, hollow, glabrous, shining, yellowish marked with reddish longitudinal lines; spores subglobose, 5 μm long, 4-5 μm broad. Pileus 5-8 cm broad; stem 5-8 cm long, 6-12 mm thick. Cespitose; growing around decaying stumps. September."

From the type specimens (NYS) the following data on microscopic characters were obtained:

Spores 5-6.5 × 3.5-4.5 μm, elliptic, smooth, not amyloid, some with vinaceous globules inside in KOH. Basidia 23-40 × 6-8 μm, 4-spored, containing vinaceous globules at times. Cystidia absent. Pileus cutis pale vinaceous in KOH, pigment encrusted on hyphae and in cell contents, hyphae cylindric, 2-4.5 μm diam.; context hyphae cylindric or inflated, 4-13 μm diam. Hymenophoral trama of undulate-subparallel hyphae, cylindric or inflated, 1.5-13 μm diam. Oleiferous hyphae present. Clamp connections absent.

The type was collected in Maine by Viola S. White. Only one basidiocarp is presently at Albany in the collection.

This species is robust and less collybioid in habit than others known in *Callistosporium,* but there is no doubt that this is the correct genus. The distinctive pigment globules in the spores, the absence of clamp connections, and a wood substrate provide the critical diagnostic characters. *Callistospermum marginatum* bears no resemblance in the field to the other species known in New England, i.e., *C. luteoolivaceum* (Berk. & Curt.) Singer (cfr. Bigelow and Barr, 1966). Instead, *C. marginatum* as described, and also in its dried state, recalls *Tricholomopsis rutilans* (Fr.) Singer. This of course is distinguished by prominent cheilocystidia, the presence of clamp connections, and a squamulose pileus.

Collybia compressiceps Bigelow, sp. nov. *Figs. 2, 5, 6.*
HOLOTYPE: **Massachusetts:** Leverett, *Cibula & Miller* (*Bigelow* 15758) (MASS).

Pileus 1-6 cm latus, convexus tum late convexus, interdum conicus et compressus, haud striatus, glaber, udus sed haud hygrophanus, asper, badius; contextus tenuis, fragilis, albidus. Lamellae adnexae, confertae vel confertissimae, angustae, pallido-bubalinae. Stipes 5-12 cm longus, 5-13 mm crassus, deorsum plerumque attenuatus et radicatus, saepe curvatus et tortuosus, cavus, striatus, sursum bubalinus, deorsum basius. Sporae (6.5-)7-9 × 3.5-4 μm, in cumulo eburneae. Cheilocystidia 21-65 × 4.5-6.5 μm, irregulariter cylindrici. Hyphae fibulatae. Lignatilis.

Pileus 1-6 cm broad, convex with an incurved margin, not striate, becoming broadly convex, sometimes conic by flattening from mutual pressure, shape ± triangular at times, slightly and broadly umbonate at times, margin often inrolled, sometimes undulate, glabrous and moist but not hygrophanous, surface uneven and with numerous small bullae, reddish brown ("chocolate" when darkest, "Hays brown" or "Kaiser brown" at times); context thin, brittle, whitish ("pale pinkish cinnamon", "pale pinkish buff"). Odor not distinctive. Taste very slightly acrid.

Fig. 2. *Collybia compressiceps* sp. nov. × 1.

Lamellae adnexed, close to crowded, narrow (up to 3 mm), forked at times, not intervenose, anastomosed at times, pale buff ("pale pinkish buff"), even and straight to eye, finely crenate to fimbriate under a lens.

Stipe 5-12 cm long, apex 5-13 mm thick, conspicuously twisted and fibrous, base usually tapered and rooting, closely appressed — slightly adherent but not forming a common fleshy mass, hollow, often curved and flexuous, thin pruinate or slight pubescence in places, soon appressed then ± longitudinally striate, pale buff above, irregularly reddish brown below, base white mycelioid and with rhizoids.

Spores (6.5-)7-9 × 3.5-4 μm, elliptic in face view, often lacrymoid in side view, smooth, not amyloid, deposit "ivory yellow". Basidia 21.5-30 × 4.5-7 μm, 4-spored. Cheilocystidia irregularly cylindric, 21-65 μm long, 4.5-6.5 μm broad, hyaline, smooth, 2-celled at times. Pileus cutis brown in KOH, pigment coarsely encrusted, hyphae cylindric, 2.5-6.5 μm diam., intermixed with subclavate end cells, ± 8 μm diam., walls usually smooth, recumbent or erect; context hyaline, hyphae usually cylindric, 4-11 μm diam., walls slightly thickened at times. Hymenophoral trama of parallel hyphae, hyaline, cylindric, 3-5 μm diam. Oleiferous hyphae present. Clamp connections present.

Cespitose. On hardwood log. August. Known only from the type collection at present.

By the stipe characteristics and its colored spore deposit, *Collybia compressiceps* obviously belongs to section *Striipedes*. There is some general resemblance to *C. fusipes* (Fries) Quélet, but this has spores 4-6 × 3-4.5 μm, a hygrophanous pileus, and broad, distant lamellae. In comparison with other taxa in the section, *C. compressiceps* is distinguished from a number of them by its relatively long spores; from the remainder, *C. compressiceps* is separated by its encrusted pigments and prominent cheilocysts in conjunction with its cespitose growth on hardwood logs.

Mycena macilenta Bigelow, sp. nov. *Figs. 3, 7-9.* HOLOTYPE: **Massachusetts:** Ruggles Pond, Wendell State Forest, *Bigelow* 15801 (MASS).

Pileus 5-35 mm latus, convexus, striatus, interdum elevatus vel lobatus, discus interdum depressus vel umbonatus, impolitus, hygrophanus, margine umbrinus dein pallido-fuligineus, discus atrofuscus dein fuligineus. Contextus succosus. Lamellae decurrentes, subdistantes vel distantes, angustae vel sublatus, cinereus. Stipes 1.5-5 cm longus, 1-2 mm crassus, succosus, pallidus vel pallido-fuligineus. Sporae 7-9(-10) × 4.5-5.5(-6.5) μm, amyloidae. Cheilocystidia 40-50 × 7-11 μm. Pilocystidia 40-100 × 10-30 μm. Lactihyphae adsunt. Hyphae fibulatae.

Pileus 5-35 mm broad, convex at first with an incurved margin, becoming broadly convex, striate, margin elevated or lobed at times, lacerate in age, disc sometimes depressed in age, rarely umbonate, surface moist and hygrophanous, dull, margin black brown at first ("Saccardo's umber" to "sepia"), disc blackish, slowly fading to pale gray brown on margin and fuliginous on disc, then opaque; context thin, firm but rather brittle, concolorous with pileus surface, watery juice when broken. Odor and taste not distinctive or odor radishlike.

Lamellae short decurrent, finally moderately decurrent, subdistant to distant, narrow to medium broad, pale cinereous to cinereous, brownish in age, edges even or uneven, not marginate.

Stipe 1.5-5 cm long, 1-2 mm thick, equal or apex slightly enlarged, brittle, with watery juice when broken, surface moist, glabrous or apex sometimes slightly pruinose, straight or curved, pallid to pale fuliginous.

Spores 7-9(-10) × 4.5-5.5(-6.5) μm (4-spored form), mostly elliptic, at times subovate or subreniform, smooth, amyloid, deposit white. Basidia 27-38 × 5.5-7.5 μm, 4-spored. Cheilocystidia scattered, broadly cylindric to basidioid or clavate, 40-50 μm long, 7-11 μm diam., hyaline or

Fig. 3. *Mycena macilenta* sp. nov. × 1.

faintly grayish, slightly refractive, protruding one third to one half of length. Pleurocystidia absent. Pileus: pilocystidia broadly cylindric, clavate, or subsaccate, 40-100 μm long, 10-30 μm diam., hyaline, smooth, dense or scattered; context hyphae cylindric or inflated, 3-19 μm diam., appearing somewhat hymeniform in radial section, walls thin or thickened, lactifers present (up to 9 μm diam.). Hymenophoral trama of interwoven to undulating-subparallel hyphae, mostly cylindric, 3-13 μm diam. Clamp connections present (4-spored form).

Scattered, gregarious or subcespitose. On *Polytrichum*, soil and needles, under *Pinus strobus* or *Alnus*. July and August.

Material examined: **Massachusetts:** *Bigelow* 15801 (type), 15709 (MASS). **Vermont:** *Bigelow* 13081 (MASS).

Mycena madorophila Bigelow, sp. nov. *Figs. 4, 10-12.* HOLOTYPE: **Massachusetts:** New Salem, *Bigelow, Bigelow & Miller* (*Bigelow* 15484) (MASS).

Pileus 8-15 mm latus, convexus vel hemisphericus dein planus, striatus, tandem discus subumbilicus et rugulosus, glaber, hygrophanus, discus fuscus, margin umbrinus, pallescens. Contextus succosus. Lamellae adnatae dein decurrentes, subdistantes vel distantes, extremis angustatae, griseus. Stipes 1.5-2.8 cm longus, 0.5-1 mm crassus, aequalis, fragilis, glaber, sordido-pallidus vel basis fuscans, succosus. Sporae 6-9 × 4-5 μm, ellipticae, leves, amyloideae. Cheilocystidia 15-35 × 6-10 μm; pleurocystidia dispersi, 15-33 × 4-6 μm. Lactihyphae adsunt. Hyphis fibulatae. Muscophilus.

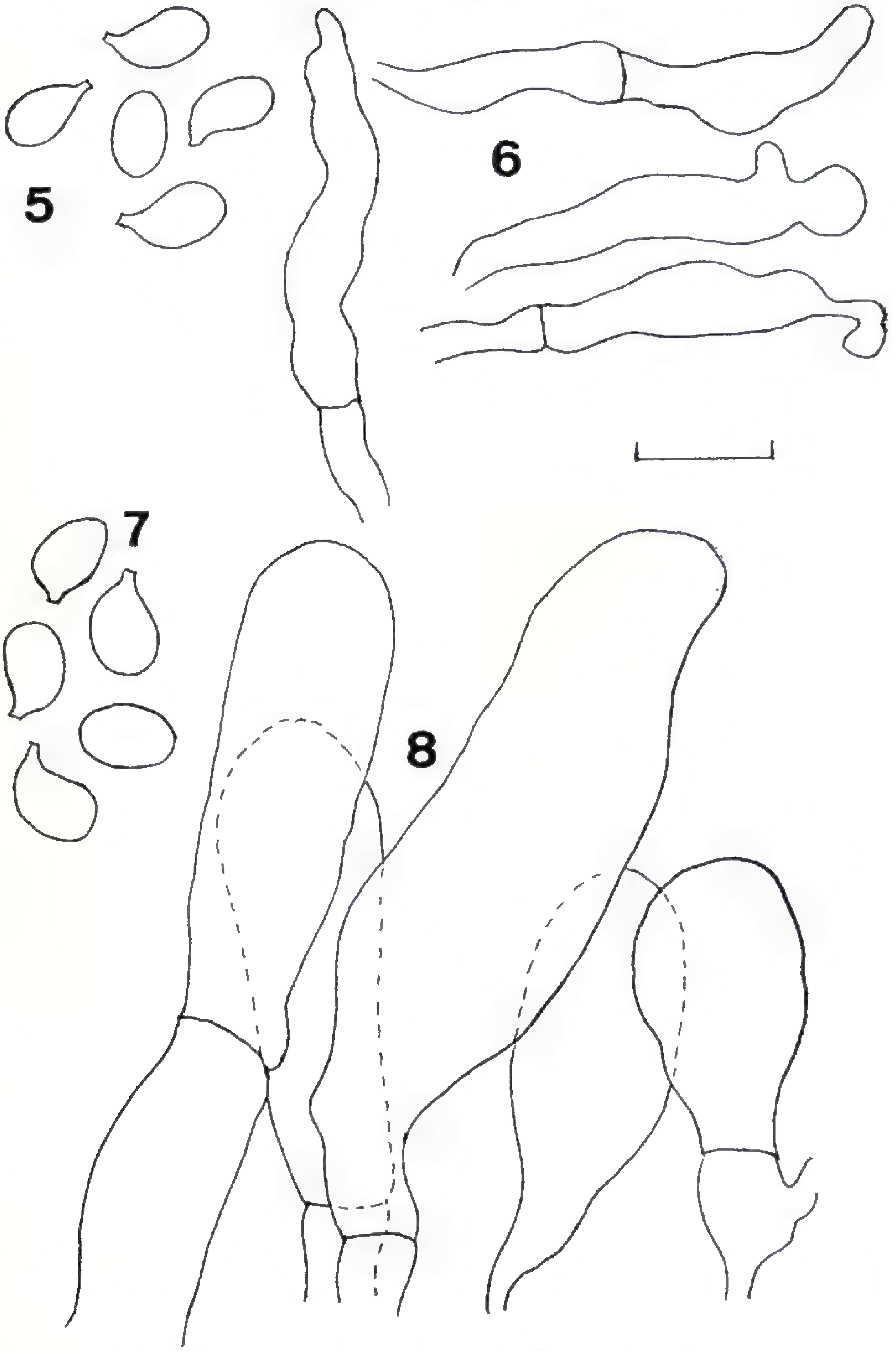
Pileus 8-15 mm broad, convex or hemispheric at first, expanding slowly to broadly convex then plane, margin striate from first, vertical but not incurved, subumbilicate in largest caps and rugulose about disc, glabrous, moist and hygrophanous, disc blackish and margin dark brown at first (nearest "Saccardo's umber"), paler with expansion then disc and striae a rather dark gray brown (nearest "buffy brown" to "olive brown"), sordid dark buff between striae, fading very slowly overall to pale gray brown; context thin, soft, concolorous with surface, watery juice when broken. Odor and taste not distinctive.

Lamellae broadly adnate then distinctly decurrent, subdistant to distant, moderately broad in center, narrow at ends, not forked or intervenose, pale gray (nearest "drab gray"), edges even and concolorous with faces.

Stipe 1.5-2.8 cm long, 0.5-1 mm thick, equal, fragile, glabrous, dingy pallid at apex, gradually darker at base with cap colors or dingy pallid the whole length, watery juice when broken.

Fig. 4. *Mycena madorophila* sp. nov. × 2.

Spores 6-9 × 4-5 μm (4-spored form), elliptic, smooth, amyloid. Basidia 22.4-43.5 × 6-8 μm, 4-spored. Cheilocystidia abundant, clavate or broad cylindric, sometimes subfusoid and ventricose, 15-35 μm long, 6-10 μm broad. Pleurocystidia scattered and inconspicuous, rather refractive, subclavate or basidioid but irregular, 15-33 μm long, 4-6 μm broad. Pileus cutis very thin, of cylindric and flexuous hyphae, 2.5-6 μm diam., cells often short, sometimes slightly inflated or nodulose, hypoderm of cells 18-40 μm broad, remainder of context of hyphae cylindric or somewhat inflated, 2-8 μm diam., numerous lactifers present (up to 11 μm diam.). Hymenophoral trama of interwoven to undulate-subparallel hyphae, cylindric or slightly inflated, 2-5 μm diam., lactifers present (up to 8 μm diam.). Clamp connections present (4-spored form).



Figs. 5 & 6. *Collybia compressiceps:* 5. spores, 6. cheilocystidia; Figs. 7 & 8. *Mycena macilenta:* 7. spores, 8. pilocystidia. standard line = 10 μm.

Solitary or scattered. On wet moss or moss-covered wood. July and August.

Material examined: **Massachusetts:** *Bigelow* 15484 (type), 15486, 15828 (MASS). **Vermont:** *Bigelow* 13378 (MASS).

The two preceding Mycenas belong to section *Hydropus* (*ss.* Smith, 1947), and they are distinguished from one another primarily by differences in cystidia. In *Mycena macilenta,* pilocystidia are present and pleurocystidia are absent, while in *M. madorophila* the pileus cutis is composed of filamentous hyphae and pleurocystidia are present. On the present collections of both species, there also appear to be distinctions in habitats, the sizes of basidiocarp, and in the degree of development in the hypodermal layers. Of additional interest is that one collection of each species had only 2-spored basidia. In *M. macilenta* (*Bigelow* 13081) the spores were the same size as in the 4-spored form, but in *M. madorophila* (*Bigelow* 13378) they were (7-)8.5-10(-11) × (4-)5-5.5(-7) μm. Clamp connections were absent at the septa of hyphae in basidiocarps of both collections.

The relationships of these two species within the section *Hydropus* seem closest to *Mycena umbrina* Smith and *Mycena marginella* var. *rugosodisca* (Peck) Smith. *Mycena macilenta* and *M. madorophila* both differ from *M. umbrina* by having lamellar cystidia and lacking caulocystidia. In comparison with *M. marginella* var. *rugosodisca,* the two species have larger spores, lack caulocystidia, and do not grow on conifer wood.

Mycena arenaria Smith also has a number of characteristics in common with *M. macilenta* and *M. madorophila,* although Smith placed *M. arenaria* in sect. *Omphalariae.* Both new species lack any caulocysts as typical of *M. arenaria.* In addition, *M. macilenta* has larger pilocysts which are mostly clavate or saccate while *M. madorophila* has a distinct hypoderm and no pilocysts — contrary to the pileus structure of *M. arenaria.*

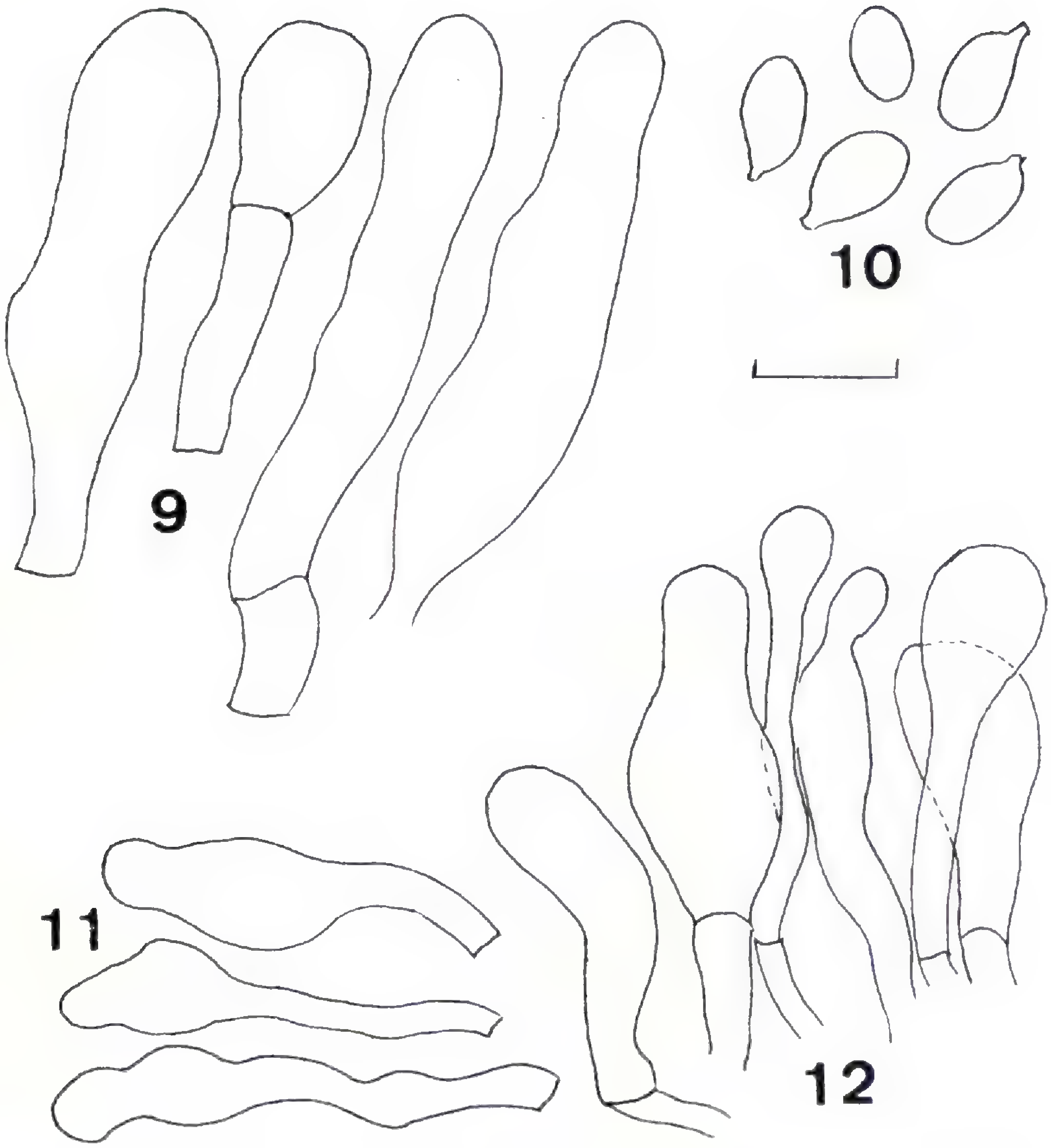


Fig. 9. *Mycena macilenta,* cheilocystidia. Figs. 10-12. *Mycena madorophila:* 10. spores, 11. pleurocystidia, 12. cheilocystidia. standard line = 10 μm.

ACKNOWLEDGMENTS

I would like to thank Stanley J. Smith, Senior Curator of Botany, New York State Museum, for the opportunity of examining the Peck herbarium. My gratitude is also extended for the support of research made possible by National Science Foundation Grant G 19534.

LITERATURE CITED

BIGELOW, H. E., & M. E. BARR. 1966. Contribution to the fungus flora of northeastern North America IV. Rhodora **68**: 175-191.

POMERLEAU, R. 1966. Les Amanites du Québec. Nat. Can. **93**: 861-887.

RIDGWAY, R. 1912. Color standards and color nomenclature. 44 pp. 53 pls. Washington, D. C.

SMITH, A. H. 1947. North American Species of *Mycena*. 521 pp. 99 pls. Univ. Michigan Press. Ann Arbor.

TANGHE, L. J., & D. M. SIMONS. 1973. *Amanita phalloides* in the eastern United States. Mycologia **65**: 99-108.

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A PORTABLE ELECTRIC HERBARIUM DRIER

ALLAN M. HALE

A problem which has consistently troubled the botanist is the drying of herbarium specimens in the field. Various methods relied on in the past include the use of kerosene lanterns (Lundell, 1956) or oil stoves (MacDaniels, 1930) to more unique drying methods employing the heat from shipboard engine rooms or placing specimen presses above an automobile engine (Fernald, 1945). These drying methods are prone to varying degrees of success, dependent on the heating method and temperature used. Fernald (1945) concluded that plant specimens dried, using artificial heat, were likely to fracture or fragment, lose natural coloration and lose some of their diagnostic characters such as glaucescence. The use of forced air, with and without heat (Maillefer, 1944) and an electric drier for herbarium specimens using heating elements (Gates, 1950) have been presented to eliminate some of the problems of specimen drying. The requirement for expedience in drying herbarium specimens while in the field is important. Botanists have become all too familiar with the results of allowing damp specimens to be transported from the field to the laboratory and observing the subsequent toll taken by molds and fungi.

The objective was to develop a portable electric herbarium drier which is durable, reliable, collapsible (Fig. 1) for easy transporting and does not present a fire or fume hazard.

MATERIALS & METHODS

The increasing importance of efficiently using limited time in the field necessitates a system which will dry specimens in a reasonable period and eliminate the effects of molds and fungi. Dimensions for the construction of this

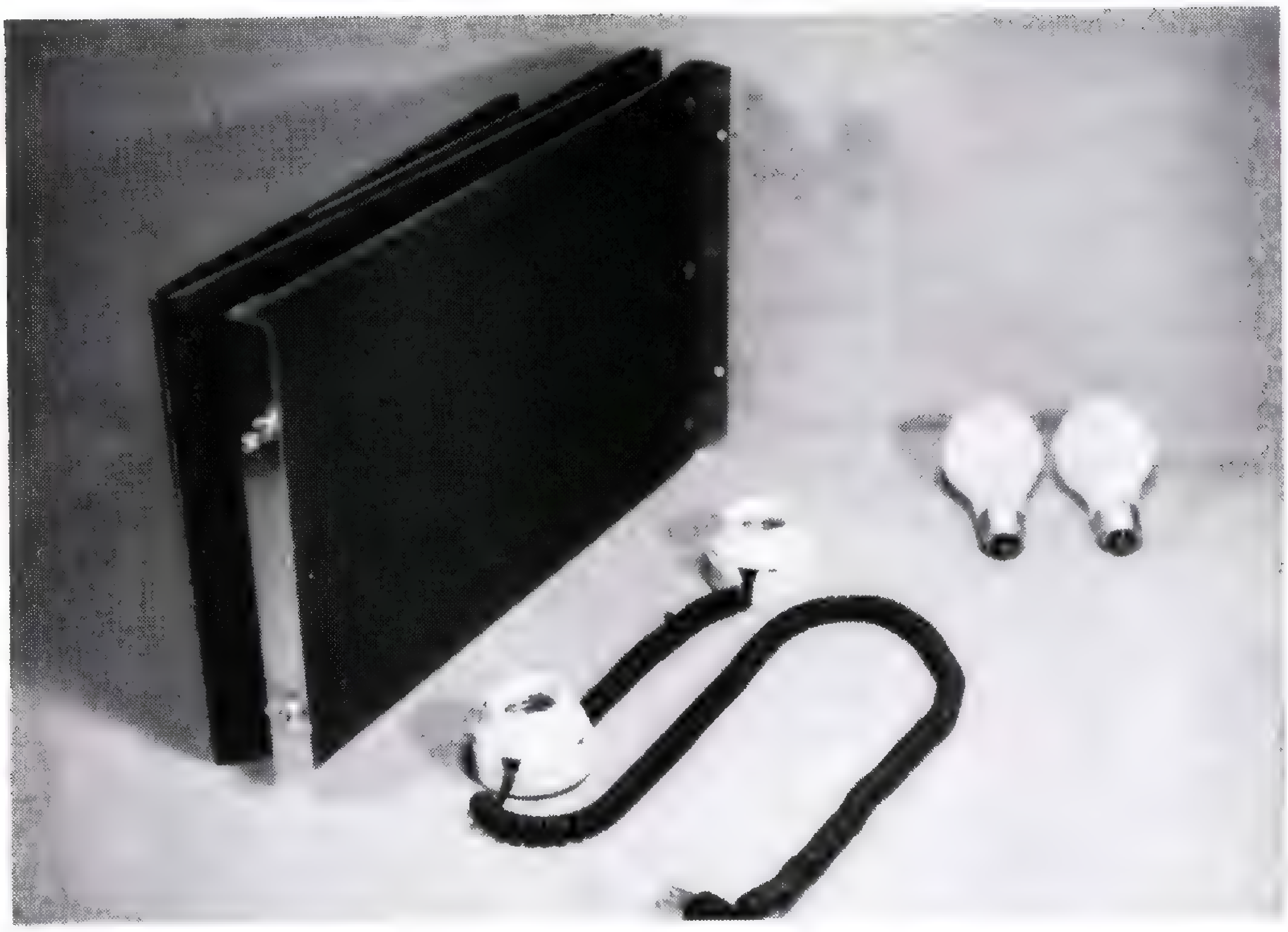

Fig. 1

plant drier are given in the accompanying drawing (Fig. 2). The drier can be built from locally available materials in one to two hours for a cost of under ten dollars. All sides of the drier are ¼-inch hardboard material. It is recommended after cutting the hardboard sides for the drier that the inside corners of the hardboard be beveled at a 45° angle for clearance when the continuous hinge is opened to assemble the drier for use. Small rivets or fasteners should be used to attach the continuous hinge and aluminum angle to the sides of the drier. It is important to alternate the placement of the fasteners for the continuous hinge to permit adequate clearance when assembled. When the aluminum angle is attached to the long side of the drier, the entire drier should be assembled to allow accurate drilling of holes for the wing-nut and screw fasteners for the removable side of the drier. After pilot holes are drilled, the holes on the interior of the hardboard sides should be countersunk to provide clearance. Two 1½-inch auger holes are drilled in the centers of the two

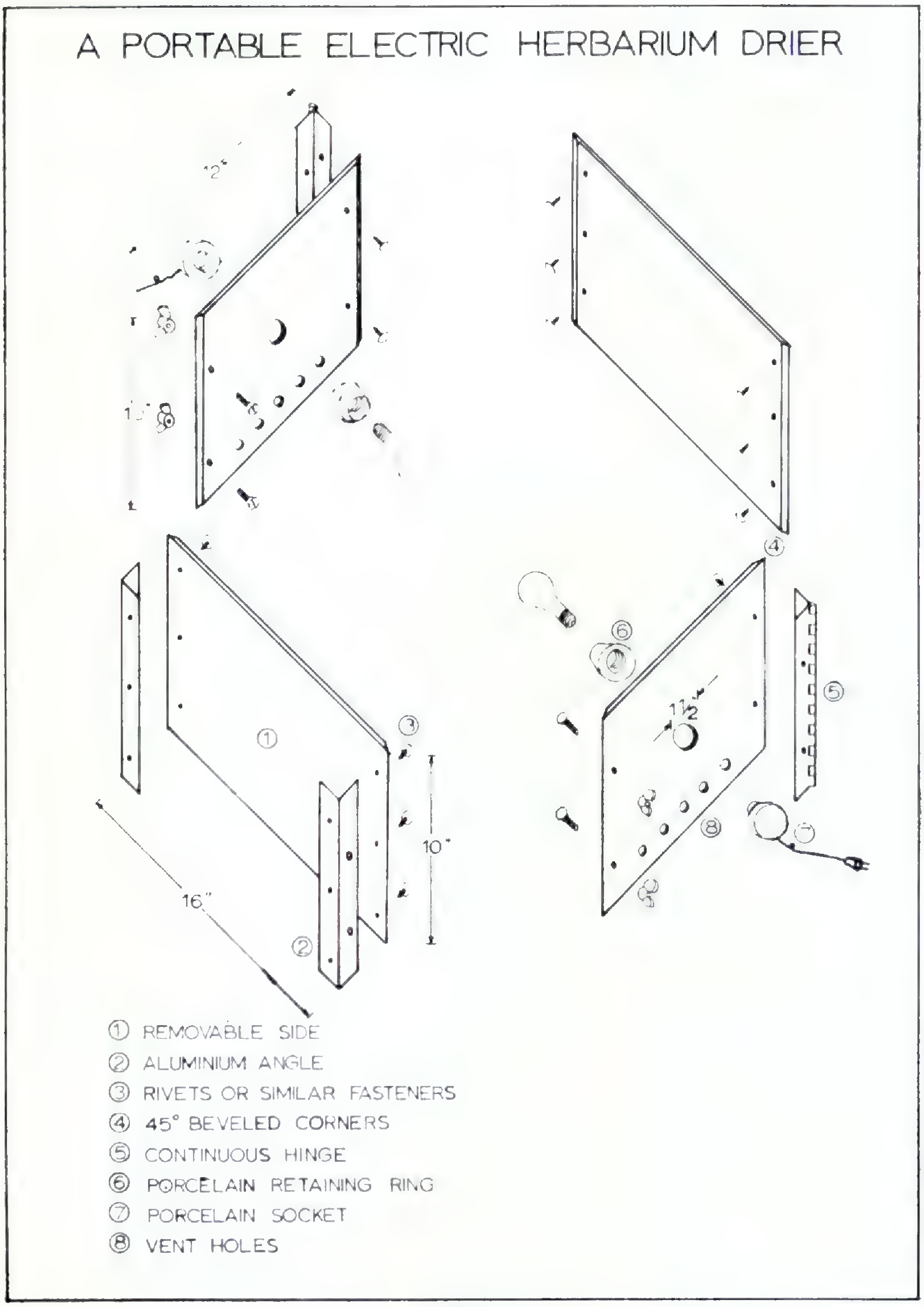
A PORTABLE ELECTRIC HERBARIUM DRIER
10"
16"
① REMOVABLE SIDE
② ALUMINIUM ANGLE
③ RIVETS OR SIMILAR FASTENERS
④ 45° BEVELED CORNERS
⑤ CONTINUOUS HINGE
⑥ PORCELAIN RETAINING RING
⑦ PORCELAIN SOCKET
⑧ VENT HOLES

Fig. 2

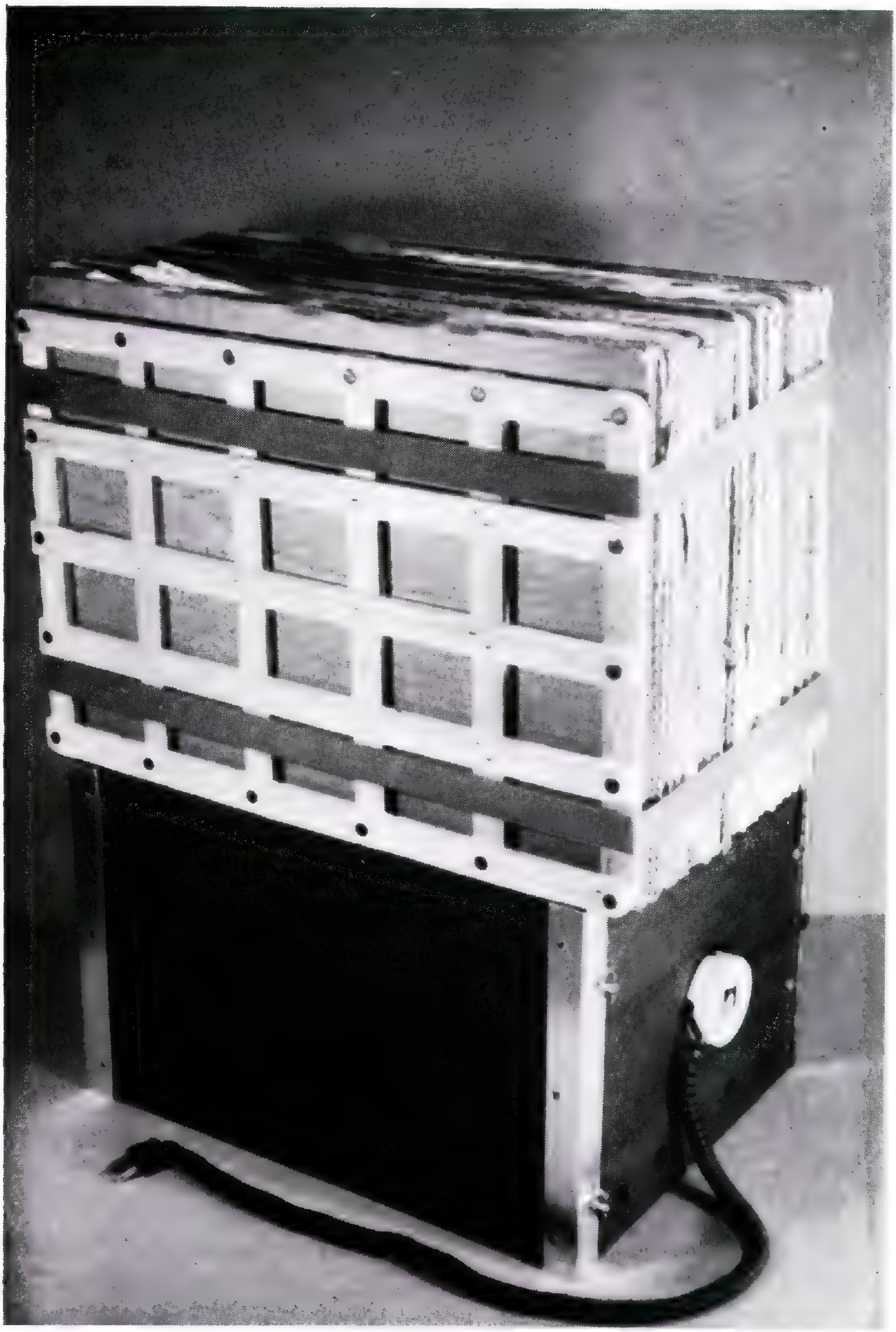

Fig. 3

short sides of the drier. A series of five ¾-inch auger holes are drilled toward the bottom of the two short sides of the drier to increase air flow. Two porcelain sockets are wired and inserted through the 1½-inch auger holes and are secured by tightening the porcelain retaining ring. The fully assembled drier is then set on a flat surface, a plant press set over the top opening and power is supplied as shown in the accompanying photograph (Fig. 3). Provision may be made for use of 6 or 12 volt D.C. automotive lamps when using power supplied from a field vehicle. The temperature and the drying time can be easily regulated by installing various wattage incandescent lamps. Further regulation of temperature is possible by using an incandescent lamp dimmer in the light circuit. By this means, the heat can be varied over a considerable range dependent on the requirements of the botanist. The circulation of heated air is by convection currents which pass through the press and carry moisture out of the press. The possibility of using a small fan was investigated but the advantages of forced air are outweighed by using the drier without fan, which is capable of drying specimens in 10-15 hours. An advantage of the convection drying system is that it provides a uniform, constant heating source.

NOTE: Open coil resistance elements of the porcelain cone variety are not recommended for use with this drier due to the possible fire hazard and the high temperatures which these coils develop.

RESULTS & DISCUSSION

The method of herbarium specimen drying described herein allows adequate time for "sweating" the specimen. In addition, blotters may be changed and "tame" specimens adjusted prior to the final drying stage, a concern of Steyermark (1947). Observation during drying of specimens indicates that control of the heat to the specimen is of utmost importance. Camp (1946) presents a qualitative but useful rule applicable here which is, "When a press is too hot for the hand it is too hot for the specimens." The

general maximum temperatures accepted in the literature vary from 102°F (Maillefer, 1944) to 120°F (Fernald, 1945). This portable herbarium drier is designed to deliver from 90°F to 120°F dependent on the wattage of the incandescent lamps used.

This portable herbarium drier has several distinct advantages over other drying methods:

1. It is portable, durable, collapsible (Fig. 3) and light weight.
2. It presents no fire or fume hazard to the specimens in the field or laboratory.
3. The heat may be varied to accommodate different specimens.
4. The drier is inexpensive to construct.

This Portable Electric Herbarium Drier was designed to adapt to a wide range of field and laboratory conditions, though modifications of this basic design can be implemented to suit the individual. Institutions or individuals with limited space and budget for herbarium drying equipment should find this a time and space saving method for the preparation of specimens.

LITERATURE CITED

CAMP, W. H. 1946. On the use of artificial heat in the preparation of herbarium specimens. Bull. Torrey Bot. Club **73**: 235-243.

FERNALD, M. L. 1945. Injury to herbarium specimens by extreme heat. Rhodora **47**: 258-260.

GATES, B. 1950. An electric drier for herbarium specimens. Rhodora **52**: 129-134.

LUNDELL, C. L. 1946. A useful method for drying plant specimens in the field. Wrightia **1**: 161-162.

MACDANIELS, L. H. 1930. A portable plant drier for tropical climates. Am. Jour. Bot. **17**: 669-670.

MAILLEFER, A. 1944. Les herborisations et la dessication des plantes pour herbiers. Bull. Soc. Vaudoise Sci. Nat. **62**: 421-429.

STEYERMARK, J. A. 1947. Notes on drying plants. Rhodora **49**: 220-227.

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DOES ARENARIA RUBELLA OCCUR ON THE BRUCE PENINSULA OF ONTARIO?

J. K. MORTON

Krotkov (1940) reported the discovery of *Arenaria rubella* (Wahlenb.) Sm. on the limestone cliffs above Driftwood Cove on the northern shores of the Bruce Peninsula. The record was published under the name *A. verna* var. *propinqua* Fern., a taxon currently referred to *A. rubella* (Fernald, 1950) or *Minuartia rubella* (Wahlenb.) Graebn. (Hultén, 1968) depending on the interpretation of the limits of the genus *Arenaria.* This record is taken up in the recent checklist of the flora of the Bruce Peninsula (Shivas et al., 1969) and by Hultén (1968). This record, if correct, is of interest because the Bruce Peninsula lies far south of the main area of distribution of this species in the arctic lowlands of North America (see map in Hultén, 1968). The species also occurs in eastern North America in isolated stations in Québec (on the south side of the St. Lawrence) and in northern Vermont.

The record of the existence of this species on the Bruce Peninsula is based on two specimens in the herbarium of the University of Toronto — *Krotkov,* 7415, collected in August 1933 and determined by Fernald in that year, and 9012, collected in August 1934 and determined by Krotkov. I examined this material a year or two ago and concluded that it was probably more correctly referable to *Arenaria stricta* Michx., but both specimens are small and probably fairly young stunted plants, which made me hesitant in my determination. This summer I visited Driftwood Cove where a study of the living plants, which are common on some parts of the limestone cliff top, confirmed my identification. Added confirmation came from a chromosome count and from cultivation of material in the garden where the plants lost some, though not all, of their stunted appearance. The diploid chromosome number of *A. stricta* and of the material from Driftwood Cove is $2n = 30$. That of

A. rubella is $2n = 24$ in the many populations which I and other workers have examined from across North America.

Morphologically *Arenaria stricta* differs from *A. rubella* in having the midvein of the leaves much stronger and more conspicuous than the marginal veins, and also in having larger seeds. Also the petals are larger, broader and more conspicuous. Unfortunately, the leaf character is not wholly reliable and overlap occurs; whilst in the very dry, exposed habitat in which the Driftwood Cove plant grows, desiccation often arrests the development of the seed. In living plants the habit differences between these species are clear cut and distinct, *A. stricta* being a diffuse, loosely tufted, long-lived perennial, often forming large mats several decimetres across, whilst *A. rubella* is a densely tufted annual or short-lived perennial forming small, tight cushions from a centimetre to nearly 2 decimetres across. Under cultivation the Driftwood Cove material assumes all the above mentioned characters of *A. stricta* and unquestionably belongs to this species — a species which is common on the limestone pavements on various parts of the Bruce Peninsula. Stunted plants similar to those at Driftwood Cove occur in other exposed habitats — e.g., on Yeo Island between the Bruce Peninsula and Manitoulin Island.

LITERATURE CITED

FERNALD, M. L. 1950. Gray's Manual of Botany. 8th ed. American Book Co. pp. 1632.

HULTÉN, E. 1968. Flora of Alaska and Neighboring Territories. Stanford University Press. pp. 1008.

KROTKOV, P. V. 1940. Botanical explorations in the Bruce Peninsula, Ontario. Trans. Royal Canadian Inst. **23**: 1, 3-65.

SHIVAS, M. S., M. D. KIRK, W. K. KIRKWOOD, & C. ROLFE. 1969. Check-list of Vascular Plants of the Bruce Peninsula. Federation of Ontario Naturalists. pp. 62.

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SPOROBOLUS AIROIDES TORREY, AN EXTENSION OF ITS RANGE IN LINCOLN, NEBRASKA SALT MARSHES

Irwin A. Ungar

Sporobolus airoides Torrey was collected at a saline location on the west side of Lincoln, Nebraska on July 1, 1968 (*Ungar* 1251, BHO). This collection site is the easternmost extension of the range of this species in Nebraska. Hitchcock (1950) reports *S. airoides* from Kansas and western Nebraska. Gates (1940) indicates that it occurs in Shawnee County, Kansas which is about 120 miles south of the Lincoln, Nebraska location. Its chief center of distribution is in the southwestern region of the United States (Hitchcock, 1950). Field research by Ungar (1970) in South Dakota and Redmann (1972) in North Dakota indicates that it is not present in saline soils in these states, and that the Nebraska station must be considered its northeastern-most extension in the eastern prairie region.

Sporobolus airoides was found growing in a single community in the Lincoln marsh area on the south side of Highway 6-2. This study site was moderately saline with a soil salinity averaging 0.2% and a median pH of 7.8. The plants made robust growth and fruiting material was found, but during the 1968 and 1969 growing seasons it did not invade the more highly saline marsh soils. Species occurring with *S. airoides* at this location included *Kochia scoparia* Schrad, *Ambrosia artemisiifolia* L., *Melilotus officinale* Lam., *Distichlis stricta* (Torr.) Rydb., *Sporobolus texanus* Vasey, and *Hordeum jubatum* L.

The introduction of *Sporobolus airoides* into this area may be due to human intervention since there is a railroad yard in this vicinity. It is certainly possible that the railroads are responsible for the long distance dispersal of *S. airoides* into eastern Nebraska. The availability of a saline site provided an ideal habitat for its establishment. The saline marsh habitats have several open ecological

niches, one of which is occupied by the introduced species *Tamarix pentandra* Pall. in the southern prairie region and the southwest. Possibly, if the distribution of *S. airoides* in southern saline locations can be used as an indicator, one could predict an expansion of *S. airoides* distribution in the Lincoln marshes, on the salt pans, or bordering the *Distichlis stricta* community.

Field studies of inland halophytes by Ungar (1965, 1970) in the prairie and plains states indicate that some species, such as *Salicornia rubra* Nels., *Suaeda depressa* (Pursh) S. Wats., *Sesuvium verrucosum* Raf., and *Distichlis stricta,* are nearly always limited to saline environments and their immediate surroundings. However, other species, such as *Hordeum jubatum, Kochia scoparia, Polygonum aviculare* L. and *Sporobolus airoides,* can be found growing under nonsaline conditions. The latter four species could be considered aggressive weeds under certain conditions.

LITERATURE CITED

Gates, F. C. 1940. Flora of Kansas. Contribution No. 291. Dept. of Botany, Kansas State College, Manhattan, Kansas. 226 pp.

Hitchcock, A. S. 1950. Manual of the grasses of the United States. U.S. Govt. Printing Office. Washington Miscellaneous Public. **200**: 1-1051.

Redmann, R. E. 1972. Plant communities and soils of an eastern North Dakota Prairie. Bull. Torrey Bot. Club. **99**: 65-76.

Ungar, I. A. 1965. An ecological study of the vegetation of the Big Salt Marsh, Stafford County, Kansas. Univ. Kansas Sci. Bull. **46**: 1-98.

————. 1970. Species-soil relationships on sulfate dominated soils in South Dakota. Amer. Midl. Nat. **83**: 343-357.

————. 1974. Inland halophytes of the United States. Pp. 235-305 in "Ecology of Halophytes". Academic Press. (R. Reimhold and W. Queen, Ed.)

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FLAT-ROCK ENDEMICS IN GRAY'S MANUAL RANGE

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In early November of 1973 we fortuitously encountered a granitic flat-rock area in Brunswick County, Virginia, whose vegetation was instantly recognized as differing from the usual type so common in the state. One peculiarity of these flat-rocks is the absence of *Selaginella rupestris* (L.) Spreng, for elsewhere in Virginia this species is a virtually ubiquitous member of the vegetation bordering expanses of siliceous rocks.

Crotonopsis elliptica Willd., *Hypericum gentianoides* (L.) BSP., *Opuntia compressa* (Salisbury) Macbride, old inflorescences of a *Minuartia,* and old rootstocks of a *Talinum* abounded. There was also a reddish *Portulaca,* old fruit stalks of an odd crassulaceous plant and a *Cyperus* resembling *C. aristatus* Rottboell, but much more robust, dominated large areas. We had by chance come upon granitic exposures whose borders and weather pits were abundantly vegetated with at least three southeastern flat-rock endemics. And oddly enough, these outcrops are within the area of intensive explorations made by Professor M. L. Fernald (1945) about three decades ago.

The odd crassulaceous plant, of course, is *Diamorpha Smallii* Britton, long considered a monotype and known on sandstone and granitic flat-rocks from Tennessee and Alabama to Georgia and the Carolinas. Although some would place the plant in the genus *Sedum,* its carpels are unique. They neatly dehisce by a vertical separation of the dorsal portion as shown in the clear and beautifully executed drawings of the late Maud H. Purdy in a paper by Svenson (1941). Moreover, because *Diamorpha* has an *n* chromosome number of 9, Baldwin (1940) suspects the genus of being an amphidiploid derived from 4- and 5-chromosome representatives of the genus *Sedum.* Both Henry Svenson, who worked with *Diamorpha* in the field

and laboratory, and J. T. Baldwin, who studied the phylogenetics of the Crassulaceae by chromosome analysis, still feel that *Diamorpha* is a valid genus (personal communications).

Seeds of *Diamorpha* which were planted in the greenhouse early in November germinated within a few days. When placed outside in the sun, the seedlings started to turn red. And when the flat-rocks were revisited in late January, shallow weather pits were already striking in appearance with their thickly-sprinkled carnelian-colored seedlings of *Diamorpha.*

The *Portulaca,* which is abundant on border zones and islands, is *P. smallii* P. Wilson, long known as a granitic flat-rock endemic. Its previously known range was from Georgia to North Carolina, and it is a relative of *P. pilosa* L. of the coastal plain.

And the third endemic, *Cyperus granitophilus* McVaugh, appears to be an exceptionally robust, aggressive, and cespitose type of *C. aristatus,* yet, two experienced and conservative cyperologists, Hugh O'Neill (1942) and Henry Svenson (personal communication), attest to its specific status. Furthermore, Murdy (1968) shows that *C. granitophilus* has consistently higher chromosome numbers, ranging from ca. 80 to 96 ($2n$), than its apparent progenitor, *C. aristatus,* which has ca. 48, 56, or 64.

I have seen *Cyperus aristatus,* a smaller plant with stipitate achenes, only from Loudoun, Fairfax, Albemarle, and Bedford counties in Virginia, and the coarser, more aggressive plant with non-stipitate achenes, *C. granitophilus,* only from these flat-rock areas of Brunswick County on the southeastern edge of the piedmont.

LITERATURE CITED

Baldwin, J. T., Jr. 1940. Cytophyletic analysis of certain annual and biennial Crassulaceae. Madroño 5: 184-192.

Fernald, M. L. 1945. Botanical specialties of the Seward Forest and adjacent areas of southeastern Virginia. Rhodora 47: 93-142; 149-182; 191-204.

MURDY, W. H. 1968. Plant speciation associated with granite outcrop communities of the southeastern piedmont. Rhodora **70**: 394-407.

O'NEILL, H. 1942. The status and distribution of some Cyperaceae in North and South America. Rhodora **44**: 43-64; 77-89.

SVENSON, H. K. 1941. Notes on the Tennessee flora. Jour. Tenn. Acad. Sci. **16**: 111-160.

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A PHOTOCOPIER AS AN AID DRAWING PLANTS

Mary I. Moore

This paper describes a technique to reproduce plant forms as silhouettes or line drawings with the aid of a photocopier. The method is accurate and acceptable where life-sized or reduced illustrations can be used. It is not generally satisfactory if enlargement of plant parts is required to show detail.

A living plant is laid on the platen of a photocopy machine such as the Xerox Model 2400. Herbarium specimens are seldom satisfactory for they are shrunken and often folded on the sheet. Plants normally do not lie flat so the cover is left open and the specimen covered with a sheet of bond paper; for white flowers a black cover will give better contrast. Plants that are larger than the machine's maximum reproduction size are printed in sections, and the resulting sheets taped together to form a complete plant.

The copy is examined for areas where line details are not clear and these are touched up with a sharp pencil using the living plant as a guide. From this copy a black and white line drawing or silhouette is made, substituting other inflorescences, leaves or plant parts when necessary to form an attractive but accurate whole. The drawing is made on semi-transparent paper using a light table and drafting pens with medium to fine nibs; use of a magnifying light improves the quality of the work. Long fine lines can be drawn with a minimum of error by using short strokes with a fine nib. The completed drawing is then photographed and reduced to a suitable size.

This technique was first used to illustrate a popular pamphlet on common grasses. It produced attractive two-dimensional illustrations of the whole plant, including the root system. The illustrations were all reduced to the same scale as an aid to identification. Since several of them

From left to right: *Hordeum jubatum*, *Dicranum polysetum* (*D. rugosum*), *Cystopteris bulbifera* and *Aralia nudicaulis*. All illustrations reduced to one quarter of original plant size.

were in excess of four feet tall, a photographic reduction to one-eighth of the original size was necessary to fit the pages of the pamphlet. Despite the extreme reduction, in only two of the twenty-four drawings did the finest lines disappear and need retouching.

The technique has since been extended to reproduce silhouettes of ferns and outlines of other plants. These illustrations are as good as, if not better than original drawings; they are not an artist's impression but an actual reproduction with accurate proportions for a given specimen.

A further refinement is possible using a reducing photocopier, such as Xerox Model 7000. The black and white drawings (if not too large) are processed through the machine one or more times so that the plants appear as one-half or one-quarter of their original size. These reduced replicas are very useful in planning and laying out illustrated articles. They are also sufficiently clear for further reproduction when limited numbers of copies are required for a special project.

It is possible for one person to collect and photocopy enough suitable material for drawings of many trees, shrubs, herbs and larger mosses in one growing season. A factor to be considered, if many plants are to be handled, is the availability of a good photocopier near the source of vegetation. In summer, for instance, a delicate fern must be picked on a cool morning and copied at once; in cool weather small or sturdy plants can be kept for a few hours in a plastic bag, or sometimes overnight in a refrigerator.

There is probably little difference in time or cost between this method and making original drawings when a taxonomist (or his assistant) has some artistic ability. The effort and skill required to collect fresh material and ink the final illustrations is the same. The real advantage is that once the material has been gathered the art work can be completed at a convenient time and secondly, that

illustrations can be produced where an artist is not available or not within the budget.

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OLD AND NEW LOCALES IN THE MAINE FLORA:

Botanical excursions in Maine during 1972 and 1973 have resulted in the discovery of plants long forgotten or unreported for many years, as well as some new plants not previously reported for the state.

Habenaria leucophaea (Nutt.) Gray. Crystal Bog, Crystal Station, Aroostook County. The Prairie Fringed Orchid was first discovered at Crystal Bog at the turn of the century. This is the only known location for this rare orchid in New England. It was collected by O. W. Knight on July 30, 1906, and by M. L. Fernald on August 24, 1907, and on August 13, 1909. No further collections were made until July 18, 1955, when Ted Wells and A. S. Pease collected *H. leucophaea* for the New England Botanical Club. On that occasion they reported seeing twenty or more plants.

The late Byron Hand of Caribou, records the following observations in his diary: July 25, 1959 — Twenty-one plants seen; July 21, 1960 — Five plants seen; 1961, No record; July 26, 1962 — No plants seen; July 31, 1963 — Three plants seen; July 31, 1964 — One plant seen.

On July 16, 1972, Ted Wells of Milton, Massachusetts, and I found six plants in flower in the open part of the bog. The orchids stood in shallow water. On a subsequent visit to the same area this past summer I did not find any plants.

Woodsia obtusa (Spreng.) Torr. Pease Mountain, Cornish, York County, August 9, 1973. While crossing the exposed ledges on the southwest side of the mountain, I came across many large clumps of this unusual fern growing in crevices with *Woodsia ilvensis.* (*Woodsia obtusa* had been found in Maine only once before, over thirty years ago, in Winthrop, Kennebeck County.)

Pease Mountain is a contact metamorphic formation in which many calcium bearing and associated minerals can

be found, such as calcite, vesuvianite, diopsite, and essonite garnet. This formation would account for the varied and unusual plants found here. The primary forest trees are *Ostrya virginiana* and *Tilia americana* with an occasional *Juniperus virginiana* var. *crebra* at the base of the mountain. The forest floor is open and rocky with thousands of *Hepatica americana* growing everywhere. Other plants of interest found on Pease Mountain are *Asplenium platyneuron, Asplenium Trichomanes, Hystrix patula, Carex platyphylla, Epipactis Helleborine, Geranium Robertianum, Arabis laevigata,* and *Conopholis americana. Hystrix patula* and *Arabis laevigata* are also new to the county.

Diplotaxis tenuifolia (L.) DC. Gilead, Oxford County, October 6, 1973. This European mustard, commonly called Wall Rocket, was found growing in railroad ballast one mile from the Shelburne, New Hampshire, line. This plant had never before been found in the state. According to Seymour's "Flora of New England", *D. tenuifolia* had not been collected in New England since 1912.

Kalmia latifolia L. Bear Den Road, Wells, York County. Mountain Laurel is one of the rarer plants found in this state. Most of the known stations previously reported have now disappeared. One of the better known occurrences was in the town of Wells. At one time *K. latifolia* could be found growing in six different areas within the town. It was last reported from Wells on June 23, 1955, when Dr. Ann Perkins led the Josselyn Botanical Society members to one such area.

Early in the fall of 1973 I was fortunate enough to meet a man from Wells who knew of an existing stand of Mountain Laurel. Following his directions, on November 10, 1973, Christopher Campbell of Orono and I found the area he described. The plants were growing in low, wet, maple woods with yews. The *Kalmia latifolia* densely covered approximately two acres. Other interesting plants growing in the immediate area were *Rhus vernix* and *Lindera benzoin.*

Specimens of the species mentioned above have been deposited in the herbaria of the University of Maine and the New England Botanical Club. Photographs were deposited in lieu of specimens in the case of *Habenaria leucophaea.*

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BAPTISIA TINCTORIA (LEGUMINOSAE) NEW TO WISCONSIN: While on a plant taxonomy class field trip on July 16, 1969, I discovered an unusual legume with chrome-yellow flowers that Dr. Hugh H. Iltis immediately identified as *Baptisia tinctoria* (L.) Vent. (Wild indigo). The plants were growing in sand on a low ridge along the south side of Rowan Creek in a village park 1½ miles west of Poynette, Columbia County, Wisconsin (SE ¼ sec. 33, T11N, R9E). Our collection (*T. Cochrane, H. Iltis, & class* 838, GH, MIL, US, UWM, WIS, and others) constitutes a new record for the flora of the state. Larisey (Ann. Mo. Bot. Gard. 27: 119-244. 1940) cited no stations between Michigan and Minnesota, and Gleason and Cronquist indicated the same disjunction (*Man. Vasc. Pls.*, p. 401. 1963). The locality nearest to the Wisconsin station is in northeastern Illinois, where according to Swink (*Pls. Chicago Region*, p. 51. 1969) *Baptisia tinctoria* was collected long ago in Cook County. The latter station marks what must be regarded as the northwestern limit of the range of the species, inasmuch as its occurrences in southeastern Minnesota (Morley, *Spring Fl. Minn.*, p. 173. 1966), southwestern Minnesota (Larisey, l. c., p. 188), and south-central Wisconsin are believed to be introductions. Since sandy areas in the southern portion of Wisconsin have been botanized thoroughly, including the very locality stated above, and since the habitat is ecologically receptive, both by its nature and by occasional human disturbance, the Wisconsin record and undoubtedly also those records from Minnesota and Florida (Larisey, l. c., p. 185) represent peripheral isolated populations which can only be interpreted as the result of sporadic long-distance dispersal.

The habitat consists of dry, fine, Plainfield sand which is occupied by an extensive, brushy *Quercus velutina* barrens. *Baptisia tinctoria* is locally quite common here, forming a loose colony scattered for 100 yards along an abandoned lane and associating with *Rumex acetosella, Talinum rugospermum, Lespedeza capitata, Amorpha canescens, Tephrosia virginiana* var. *holosericea, Euphorbia corollata,*

Ceanothus americanus, Aureolaria pedicularia var. *ambigens,* and *Antennaria neglecta.* I returned to the area with a companion during mid-August, 1970 (*T. Cochrane & B. Warnes* 2097, 19 Aug. 1970, WIS), and early September, 1973 (*T. Cochrane & B. Cochrane* 5749, 2 Sept. 1973, MICH, MIN, WIS), and observed that the wild indigo was forming fruits. Forty-two plants were counted, the largest with 22 stems from the base and up to 1.1 m tall. Some were small, single stemmed and without flowers, indicating that the plants are reproducing. Additional associates seen at the time of the second visit were *Helianthemum canadense, Lithospermum caroliniense, Pedicularis canadensis, Rudbeckia hirta, Gnaphalium obtusifolium,* and *Solidago nemoralis.* Later in the season *Aster azureus* was in full bloom, making it the most showy species present; but the *Baptisia* dominated the herbaceous flora by its size, while the grasses dominated by their numbers. In the driest parts of the area *Eragrostis spectabilis* was the most common grass, with *Leptoloma cognatum, Koeleria macrantha, Bouteloua hirsuta,* and *Andropogon scoparius* also being important components of the vegetation. Other graminoids included *Juncus tenuis, Cyperus filiculmis* var. *macilentus, Carex muhlenbergii, Agropyron repens, A. trachycaulum* var. *glaucum, Sporobolus cryptandrus, Aristida basiramea, Sorghastrum nutans, Digitaria sanguinalis,* and *Panicum virgatum.* The oak barrens habitat is frequently described as being of "sterile" quality because its very sandy soils have high temperatures, low water supply, and lack nutrients. Yet in Wisconsin the barrens flora cannot be fairly characterized as depauperate, since it contains fully 70% as many species as comprise the state's dry forests, 88% as many as the more mesic oak openings, and 21% more than the dry prairies.

Larger leaflets in our material of *Baptisia tinctoria* are 1.5-2.6 cm long and 0.9-1.3 cm wide, fitting the description of var. *crebra* Fern. This variety was maintained by its author (Fernald, Rhodora 47: 94. 1945; *Gray's Man.,* ed. 8, p. 887. 1950) and by the monographer (Larisey, 1. c.,

p. 185) ; others state (Clausen, Rhodora **46**: 281. 1944) or imply (Gleason & Cronquist, 1. c.) that a separate name for those individuals larger in habit and leaf dimensions is not justified.

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TWO NOMENCLATURAL CHANGES IN SENECIO: Some recent bibliographic work in *Senecio* has revealed two forgotten specific epithets which have nomenclatural priority over two widely-known names. The type specimens for both were located in the British Museum by Dr. Arthur Cronquist, and photographs were supplied through the kindness of J. F. M. Cannon, Deputy Keeper of the Department of Botany, British Museum (Natural History).

Senecio schweinitzianus Nutt. (Trans. Am. Phil. Soc. 7: 413. 1841) must replace the familiar *S. robbinsii* Oakes ex Rusby (Bull. Torrey Club **20**: 19. 1893). The original publication of *S. schweinitzianus* describes it as being "In Arkansas, and, according to Schweinitz, in Carolina, marked *S. caroliniana* in his herbarium, but not, apparently, the plant of Sprengel." The holotype (in herb. BM) bears the following inscriptions: "*Senecio *schweinitzianus*" (with Nuttall's well-known asterisk indicating a new entity) and "*S. carolinianus* Schw." The specimen consists of a flowering stem with two attached and one unattached basal leaves plus two cauline leaves, providing no doubt that it belongs in the entity long-called *S. robbinsii*. This taxon occurs primarily in New England and adjacent Canada and New York, but it is also well known on the Appalachian mountain tops of western North Carolina, e.g., Roan Mountain (cf. Barkley, Trans. Kans. Acad. Sci. **65**: 318-408. 1962).

Senecio cymbalaria Pursh (Fl. Am. Sept. 2: 530. 1814) must replace *S. resedifolius* Less. (Linnaea **6**: 243. 1831), which in turn is based upon *Cineraria lyrata* Ledeb. (Mem. Acad. Petersb. 5: 576. 1818). The original description notes the locality as "On the northwest Coast. *D. Nelson* in herb Banks." The holotype is in the collection of Sir Joseph Banks in the herbarium of the British Museum, and written *on the back* of the specimen is the following: "Northwest Coast of America, Cape Newnham, Mr. Nelson." Cape Newnham (i.e., Cape Newenham) is in southwestern Alaska at approximately 59°N, 162°W. The type consists of four small plants mounted on the single sheet;

each plant has the characteristic "boreal aspect" and falls easily within the circumscription of the taxon, which is called *S. resedifolius* elsewhere (Barkley, op. cit.).

Detailed synonomies for these two taxa are included in the forthcoming treatment of *Senecio* for the North American Flora, to be published by the New York Botanical Garden.

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ELEOCHARIS PARVULA (R. & S.) LINK NEW TO ILLINOIS: The wide ranging *Eleocharis parvula* (R. & S.) Link is represented in eastern North America only by variety *parvula*, which occurs in wet saline soils mostly along the east coast from Newfoundland south to Florida and Texas. A few inland stations have also been reported for this variety, but in the central United States its distribution is limited and very sporadic. Svenson (1929, 1934), in an extensive study of the genus, reported that he had seen no specimens of *E. parvula* var. *parvula* from the interior except from New York and Michigan. Later, Fernald (1950) included Minnesota in this list, while more recently Steyermark (1963) reported its occurrence in five counties in Missouri. The authors have recently found this variety growing in east-central Illinois. The population of *E. parvula* var. *parvula* was found growing on a fairly level, muddy beach at the south edge of a small pond. The beach, which had been revealed by the low level of the pond, was caused by a prolonged summer drought. It was nearly covered by a green carpet of this species which extended over an area about 12 m long and 3 m wide. A number of common shoreline species were found scattered among this carpet of *E. parvula*. These included *Cyperus acuminatus* Torr. & Hook., *Cyperus ferruginescens* Boeck., *Eleocharis obtusa* (Wild.) Schult., *Ammannia coccinea* Rottb., *Rotala ramosior* (L.) Koehne., *Bidens frondosa* L., *Xanthium commune* Britt., and *Phyla lanceolata* (Michx.) Greene. **Illinois:** COLES COUNTY: beach of a small pond just east of Charleston at the edge of state route 16 (NW¼, Sect. 13, R9E, T12N), 4 October 1973, *Ebinger & Nyboer* 14005 (EIU); 9 October 1973, *Ebinger & Nyboer* 14089 (EIU, ILLS, ISM, SIU).

LITERATURE CITED

FERNALD, M. L. 1950. Gray's Manual of Botany. 8th Ed. American Book Co. New York.

STEYERMARK, J. A. 1963. Flora of Missouri. Iowa State Univ. Press. Ames.

SVENSON, H. K. 1929. Monographic studies in the genus *Eleocharis.* Rhodora **31**: 167-191.

————. 1934. Monographic studies in Eleocharis. III. 1. The eastern American segregate of *Eleocharis pauciflora.* Rhodora **36**: 377-389.

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THE ANDROECIUM OF SURIANA MARITIMA

Almuth H. Tschunko and Norton H. Nickerson[1]

One member of the flora of the Jewfish Chain in the central Bahamas, the flora of which will be more fully described elsewhere (Nickerson et al., 1976) is *Suriana maritima* L., the Bay Cedar, a shrub found along open shores above high-tide line. Petal fall and stamen drop occur within 6 hours of early-morning anthesis. In January, 1971, half-way through the five-month winter dry season, 20 flowers and buds from three plants on Hummingbird (Jewfish) Cay and 15 from two plants on Coakley Cay (the two islands lie about four miles apart in the Jewfish Chain) were dissected and compared in the laboratory. In January, 1972, 32 buds from 7 plants on Hummingbird Cay and 25 buds from 4 plants on Coakley Cay were dissected while still unopened and attached to the plants. No differences in androecial patterns occurred in comparisons between either successive years or different islands.

Britton and Millspaugh (1920) described this monotypic taxon as having 10 stamens. We found the number of stamens per flower to range from 5 to 8; no bud or flower ever had 10 stamens but always had at least 5. The remaining 5 members of the androecium, if present, consisted of combinations of fertile stamens and staminodia. On both Coakley Cay and Hummingbird Cay, the most commonly-occurring androecial situation in 92 flowers examined was 5 stamens and 5 staminodia. The range was from 5 and 0 to 8 and 1 for stamens and staminodia, respectively. The five fertile stamens were always very slightly inward of any outer row members and always opposite the sepals (thus obdiplostemonous), and had long subulate filaments The remaining (outer row) members of the androecium were always opposite the petals, their subulate filaments

[1]This study was supported by grants made to Tufts University by the Hurdle Hill Foundation and the Arnold Bernhard Foundation.

were invariably shorter and, if present, the anthers easily abscised. Staminodia were the same size and shape as the filaments of these shorter stamens.

Britton and Millspaugh (1920) cited Lindley (1836), which we could not obtain for examination. In Lindley's (1847) 2nd edition of the *Vegetable Kingdom,* he quoted for *Suriana* his own first edition of the same book (1837) as follows: "Stamens indefinite, hypogynous, placed in a single row; filaments subulate"; he quoted Arnott (1834), with confirmation attributed to Endlicher, that "stamens are opposite the (5) sepals." Lindley figured only one stamen, which he had adapted from an unnamed 1820 source. Arnott's (1834) description was: ". . . stamens 5, alternate with the petals, sometimes with 5 alternating ones that are occasionally abortive, all inserted with the petals, filaments persistent, distinct, subulate from a broad base. . . ." Our findings support this description in part. Earlier, Linnaeus (1753), in his *Species Plantarum,* classified *Suriana* in his *Pentandria Pentagynia.* In Edition 2 of his *Genera Plantarum* (1742), Linnaeus noted, for *Suriana,* "filaments 5"; again in Edition 5, 1754, his observation was the same. Yet in Edition 6 (1764) Linnaeus classified *Suriana* under the *Decandria Pentagynia.* Possibly he assumed the missing members or parts were lost in the handling of his specimens.

Airey-Shaw's (1966) compendium incorrectly cited Gutzwiller's 1961 study, conducted on 41 preserved flowers from Florida and Cuba. She observed that the stamens were obdiplostemonous, with those of the outer row sometimes sterile and sometimes missing. Those of the inner row she found always to be fertile. Her findings are in agreement with ours, but she did not mention filament size differences between the two rows. The amended description of *Suriana maritima* L., family Surianaceae, is: Obdiplostemonous androecium of 5 (up to 10) fertile members inserted just above the petals; stamens opposite the sepals 5, with subulate filaments: stamens or staminodia opposite the petals 0-5, with shorter subulate filaments.

LITERATURE CITED

AIREY-SHAW, J. K. 1966. Willis' Dictionary of the Flowering Plants and Ferns. Ed. 7. Cambridge Univ. Press. 1214 pp.

ARNOTT, H. J. 1834. Surianae. *In:* WIGHT & ARNOTT. Prodromus I. London.

BRITTON, N. L. & C. F. MILLSPAUGH. 1920. The Bahama Flora. (Reprint ed., 1962) Hafner Publishing Co., Inc.; New York. 695 pp.

GUTZWILLER, M-A. 1961. Die Phylogenetische Stellung v. *Suriana maritima* L. Bot. Jahrb. Engl. **81**: 1-49.

LINDLEY, J. 1836. A natural system of botany. II. Surianaceae. p. 142. London (not seen).

————. 1837. The vegetable kingdom. London.

————. 1847. The vegetable kingdom. Ed. 2. London.

LINNAEUS, C. 1742. Genera Plantarum. Ed. 2. Leiden.

————. 1753. Species Plantarum. (Reprint.) Stechert-Hafner Publishing Co. Inc.; New York.

————. 1754. Genera Plantarum. Ed. 5. Stockholm.

————. 1764. Genera Plantarum. Ed. 6. Stockholm.

NICKERSON, N. H., J. C. SEMPLE, R. A. HOWARD, A. TSCHUNKO, & W. PHIPPEN. (1976). Ecology and Vegetation of Hummingbird Cay, Jewfish Chain, Great Exuma, Bahamas. (in prep.)

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A small fund for the benefit of RHODORA has been established in memory of Stuart Kimball Harris, an Associate Editor of this Journal for many years. He also served the New England Botanical Club as its Recording Secretary for repeated terms of office, as a member of the Council, and as President at the time of his death.

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FLORAL BIOLOGY OF PROBOSCIDEA LOUISIANICA (MARTYNIACEAE)

JOHN W. THIERET

In July 1973, while on the faculty of the University of Oklahoma Biological Station, I studied the floral biology of the unicorn plant, *Proboscidea louisianica* (Miller) Thellung. A few additional observations were made in August, 1974, in Salt Lake City, Utah, on plants of this species in a home garden. Results of my study are reported in this paper. Previously I had sought in vain for published information on most aspects of this subject. Bracketed data below refer only to Utah plants; otherwise, the account is based on Oklahoma plants although almost all data apply to western *Proboscidea* as well.

The ten individual Oklahoma plants observed were in a sandy grazed field overlooking Lake Texoma, 1 mile west of Willis and 2 miles west of the Biological Station, Marshall County. In addition to the unicorn plants, prominent forbs in the field were *Cnidoscolus texanus, Monarda punctata, Helenium amarum,* and *Verbesina encelioides.* Grasses included *Axonopus affinis, Cenchrus pauciflorus, Cynodon dactylon, Eragrostis sessilispica,* and *Tridens albescens.* Observations were begun on 1 July and were concluded on 21 July. During the first three days (not successive), I watched the flowers for a half-hour period every four hours throughout the day. Because no insect or other visitors to the flowers were noted at night, I thereafter confined my observations mostly to daylight hours.

Thirty-five flowers — at least three from each of the 10 plants — were tagged and numbered for study of time and pattern of opening, duration of anthesis, and early stages of fruit development. Every time I observed these flowers I examined the stigmas for the presence of pollen. Additional data collected from tagged and also from untagged flowers included flower color and odor, kinds of insect visitors, and duration and pattern of their visits. Insects were caught in a 1-inch-wide killing vial placed over the throat of the corolla; the vial was quickly capped as the insect backed into it from the corolla tube.

FLOWERS

A "face" view and a side view of a unicorn plant flower are shown in Figure 1. The flowers of *Proboscidea louisianica*, each bracteate at the base of its pedicel and bibracteolate at the base of its calyx, are in several-flowered, terminal, erect racemes. The bracts are deciduous at or even before the beginning of anthesis. [In the Utah plants they persisted longer — until the fruits were 3-6 cm long.] A single raceme may show floral development from unopened buds distally to full-sized fruits proximally. The axis of the raceme elongates as the fruits mature.

The synsepalous, somewhat zygomorphic calyx is five-lobed and is split to the base between the two lowermost lobes. It is deciduous soon after anthesis. [In Utah plants, many calices persisted until the fruits were nearly full sized.] The corolla tube is narrowly cylindrical at its base but rather abruptly widens at about the level of the top of the ovary; from there it is narrowly campanulate. The corolla limb is five-lobed, the two upper lobes erect, the two lateral lobes spreading to reflexed, and the lower lobe projecting forward in the plane of the tube. The upper lobes of the corolla are external in bud and overlap each other and the lateral lobes. The laterals overlap the lower lobe, which is completely internal. Just prior to anthesis, the corolla in bud is very pale whitish yellow, sometimes

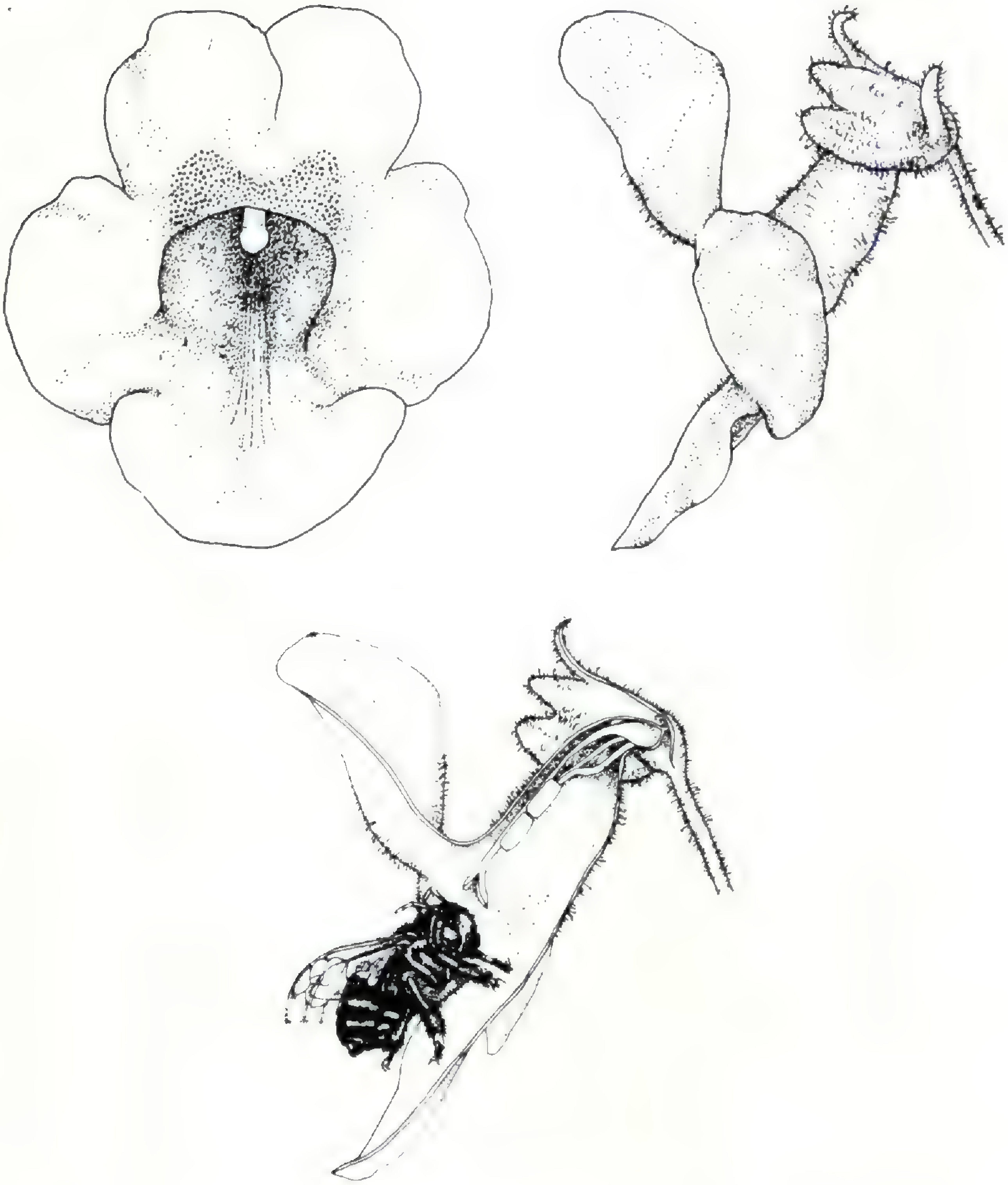

Fig. 1. Flower of *Proboscidea louisianica.* Upper left: "face" view. Upper right: side view. Lower: cutaway view, showing *Melissodes communis* alighting on lower lip.

tinged with green. As the corolla opens, the yellow and green disappear. At full anthesis the corolla is white with a pink tinge that increases with age. Orange guidelines arise centrally on the lower lobe and extend back along the lower side of the tube to between the bases of the lower pair of stamens. Minuscule purplish dots sprinkle the

inside of the tube and spill over onto the corolla throat and onto the bases of the two upper lobes; those on the lobes are larger than the others.

The four stamens are didynamous and epipetalous. In bud the anthers are free from each other and each is bent into a broad "V." As the flower develops, the filaments lengthen and the anthers straighten. The anthers of each pair become connate side to side; tips of the anthers of one pair of stamens become connate to adjacent tips of the anthers of the other pair. By anthesis, the "anther box" (as I call the structure composed of the connate anthers) is positioned midway on the upper surface of the corolla tube behind the stigma and the distal portion of the style. Opening of the anthers occurs by longitudinal dehiscence of the anther walls on the side facing the axis of the tube. A mass of pollen is thus precisely in place for some of it to be picked up by the hairs on the backs of pollinating insects ascending the tube. Stages in the development of the anther box are shown in Figure 2.

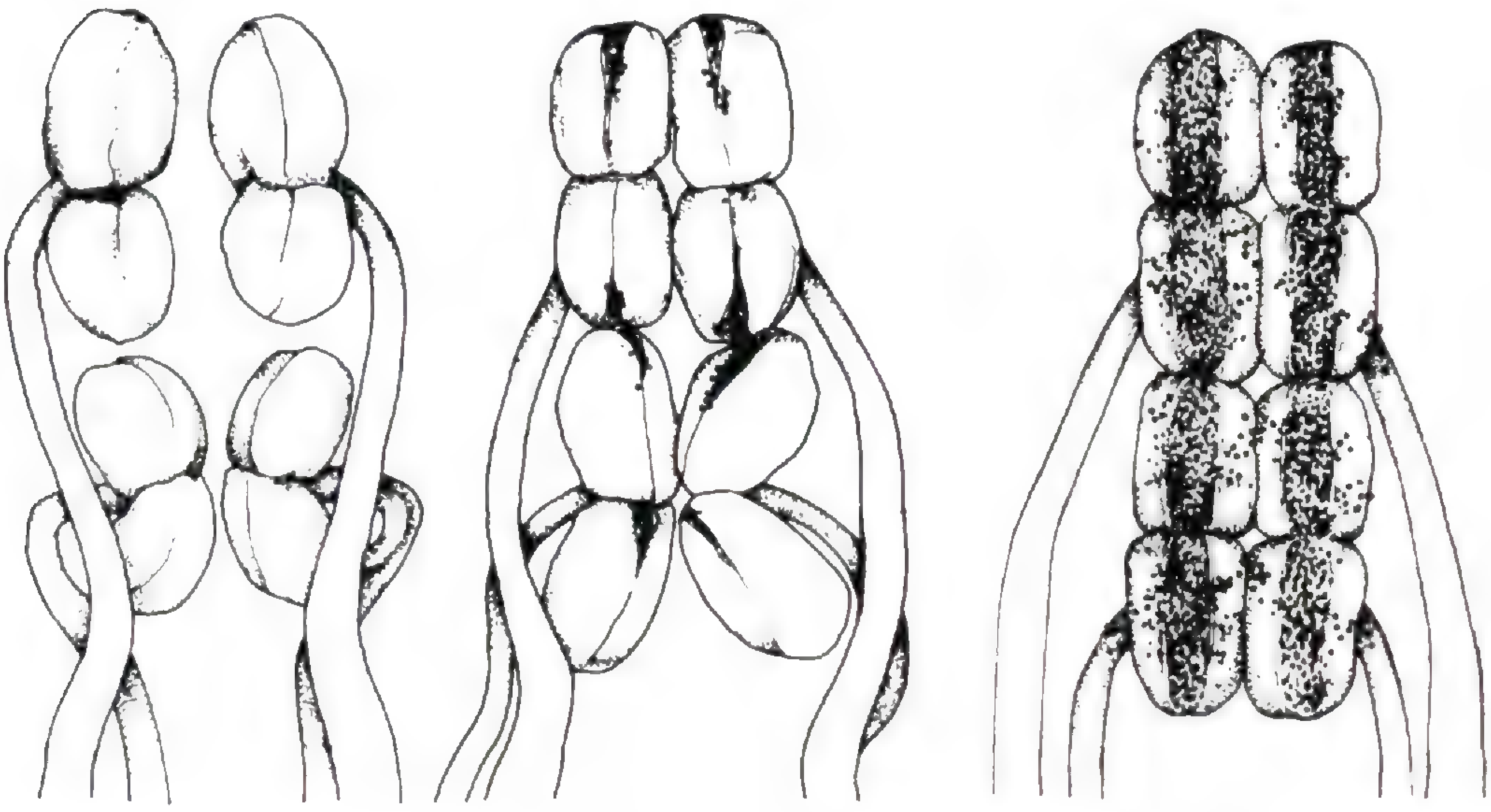

Fig. 2. Stages in the development of the anther box of *Proboscidea louisianica*. Left: young stage, the anthers not yet in contact and not yet dehisced. Center: somewhat older stage, anther contact and dehiscence beginning. Right: at beginning of anthesis, anthers in contact and fully dehisced.

In every flower I examined, a staminode (a fleshy protuberance about 1.5-3 mm long) occupied the place of the fifth stamen. That the staminode may sometimes be lacking is suggested by some descriptions of *Proboscidea* flowers that fail to mention it, although I prefer to think this results from faulty observation of floral morphology.

The ovary is bicarpellate and unilocular; each of its two placentae is intruded and expanded into a broad lamella. The slender style is about thrice as long as the ovary. The stigma, positioned well in front of the anther box, is sensitive to even the slightest touch, its two flat lips, with their receptive inner surfaces, closing together rapidly (within about 2 seconds). After about 5 minutes (in the first of a series of touches) the lips will have spread apart again. Opening and closing of the lips occur mainly because of movement of the lower lip. When the lips are open, the lower one is in position to "scoop" pollen from the back of an insect passing beneath it. Immediately after so doing, it closes against the upper one, trapping the pollen between them and thus preventing its possible dislodging as the insect leaves the flower. The closing of the lips also may prevent or significantly reduce transfer of pollen of a flower to the stigma of that flower by the exiting insect — the receptive surfaces of the stigma are simply not exposed. When the lips are well covered with pollen, they do not reopen.

In a series of touches, the time required for closing of the lips increases hardly at all, but the time for their spreading apart again increases considerably, resulting in the phenomenon of stigmatic "fatigue." In four flowers, each on a different plant, I observed stigma response to eight successive touches, each touch (after the first) being made after the lips had returned to the fully open position. The average times required for this return were: Touch I — 5 minutes; II — 8 minutes; III — 15 minutes; IV — 18 minutes; V — 18 minutes; VI — 20 minutes; VII — 25 minutes; and VIII — 25 minutes. Observation of "fatigue"

in the stigma was halted after eight touches because of fatigue on the part of the observer.

Glandular hairs, producing a copious, viscous, and sweet secretion, are abundant on the bases of the filaments and on the area of the corolla tube between the bases of the filaments. No secretion was noted elsewhere in the flower. It is presumably this secretion that pollinators seek, although I was unable to demonstrate this (stomach analysis of pollinators of the unicorn plant should be carried out).

At full anthesis the pedicel is ascending, forming a 35° - 45° angle with the vertical (i.e., the axis of the raceme). The calyx is nearly 90° from the vertical. The corolla, however, is sharply declined, its tube and lower lobe being at about 135°, so that visiting insects must move upward into the tube. In a single raceme I saw no more than three flowers in anthesis at one time; usually there was only one, infrequently two.

The flowers typically begin to open in the afternoon, mostly at about 6:00 PM but occasionally as early as 1:00 PM or as late as 11:00 PM. As opening proceeds, the upper lobes of the corolla become directed forward, exposing the lateral lobes. The laterals then become directed forward, exposing the lower lobe. Finally the lower lobe, too, assumes the forward position, which it retains. The upper lobes become gradually erect as the laterals spread or become somewhat reflexed. The opening process lasts from 3 to 6 hours.

The anthers have dehisced by the time the flower is half open. The lips of the stigma, however, do not part until the flower opens fully.

The odor of the flowers is difficult to describe. Somewhat unpleasant, rather penetrating, it was characterized by an Oklahoma colleague as "aminoid." I cannot improve upon this description. The secretion from the glandular hairs covering the stem and leaves imparts to hands that handle the plant an odor similar to that of the flowers.

Once a flower is open it stays so for the duration of anthesis. Most flowers last about 40 hours, the corolla

dropping suddenly — usually at about noon to 3:00 PM of the third day. Flowers on some plants, however, may last only 30-36 hours. Within 24 hours after corolla fall, the pedicel moves to about 90° from the vertical. Within another day it becomes reflexed to about 135°, the position it retains during fruit development.

Flowers on individual plants behave similarly with respect to opening time, time required for the flowers to open fully, and duration of anthesis. This suggests that these may be genetically-controlled features.

INSECT VISITORS

Visitors to the flowers were infrequent and all were bees (Hymenoptera, Apoidea); many flowers appeared not to be visited at all, as evidenced by the lack of pollen on their stigmas. Pollinators were the following:

Family Anthophoridae
- *Anthophora occidentalis* Cresson
- *Centris subhyalina* Fox
- *Mellisodes communis* Cresson

Family Halictidae
- *Augochlorella striata* (Provancher)

[In the Utah plants the only pollinator taken was *Bombus fervidus* (Fabricius), of the family Apidae.]

These fast flying bees behaved similarly during visits to the flowers. Landing on the lower lip (see Figure 1), they quickly ascended the corolla tube, first brushing against the stigma, the lips of which then closed, and then against the anther box. Several (5-8) seconds later, they backed out of the tube and resumed flight, usually, but not always, going to another *Proboscidea* flower on the same or on a different plant. The amount of pollen deposited on the stigma as the result of a single visit of a bee varied from many grains (55, in one count) to almost none, depending on how much pollen the insect was carrying. The bees taken as specimens showed most pollen adhering to the hairs on top of the thorax but also some on those of the

face, abdomen, and legs. The pollen baskets (corbiculae) on some of the specimens were full of *Proboscidea* pollen — and, in some instances, of other, unidentified kinds as well.

Several small bees of the genus *Lasioglossum* (family Halictidae) visited *Proboscidea* flowers but were not pollinators. They landed on the lower or lateral lobes and walked immediately to the anther box, from which they took pollen and packed it into their pollen baskets. At no time did they contact the stigma or even the style.

Unicorn plants are markedly viscid pubescent on the stems and leaves. The glandular hairs entrap many minute insects (including thrips, fairyflies and other Hymenoptera, *Drosophila* and other Diptera, aphids, Hemiptera, and weevils and other Coleoptera).

POLLINATION EXPERIMENTS

An exclusion experiment was set up by erecting a crude "tent" of cheesecloth around a large *Proboscidea* plant. The tent effectively excluded the bees that, by that time, I had recognized as pollinators. During the 14 days of the experiment, eight flowers on the enclosed plant came into and passed anthesis. One of these I pollinated by hand with pollen from a flower in a neighboring raceme on the same plant; it did not set fruit. Another one I pollinated by hand with pollen from another plant; it set fruit. The six other flowers, unpollinated, dropped soon after anthesis.

In an additional mini-experiment I pollinated, with its own pollen, a flower on each of three plants and then bagged each flower to exclude all other pollen. These flowers produced no fruits.

[In Utah, I pollinated four newly-opened and previously-unpollinated *Proboscidea* flowers on one plant: flower 1, with its own pollen; flower 2, with pollen from another flower on the same plant; and flowers 3 and 4, with pollen from another plant. The flowers were then bagged to exclude insects. Flowers 1 and 2 set no fruit; flowers 3 and 4 had developed fruits 6 cm long by the time my observations of them were concluded.]

The results of these limited experiments suggest (1) that *Proboscidea louisianica* fruits do not develop in the absence of pollination and (2) that pollination of a flower of this species with its own pollen or with pollen from another flower on the same plant is fruitless. Further such studies, however, are obviously necessary to reach definite conclusions.

FRUITS

Twenty-three of the tagged flowers produced no fruits. Instead, they dropped, pedicel and all, within 3 days after the corollas fell. On the stigmas of these flowers I had observed no pollen or but a few grains.

Fruit development in the other tagged flowers, each of which had been well pollinated by bees, was rapid, at least in the early stages observed by me. Three days after corolla fall, the fruits begin to protrude from the calyx. Three days later, they were as much as 6 cm long, and the calyx had dropped. At this point my observations of developing fruits were halted — my teaching assignment at the Biological Station was over. However, seemingly nearly mature fruits were carried to my home laboratory in the hope that, as they dried out, they would behave as if they were *in situ* at Lake Texoma. I believe that they did just this. Additionally, many last year's fruits were collected from the ground for study.

At maturity — but before drying and dehiscence — the fruits have a body 6 - 10 cm long and 2 - 3 cm thick and an arcuately-upcurved, slender beak 1.5 - 3 times as long as the body. During drying of the fruit, the exocarp, starting along the upper suture, sloughs off in two valves, revealing the stony, sculptured endocarp and the intricate crest (see Figure 3). The beak splits longitudinally into two sharp-pointed, hooked "horns." With further drying, these "horns" become oriented in such a way that they are reminiscent of mammoth tusks with their tips pointing toward each other or, when extremely dry, even overlapping.

Fig. 3. Fruits of *Proboscidea louisianica.* Upper left: fruit not yet shed from plant, splitting of exocarp beginning to reveal crest. Lower left: fruit shed, lying on ground, exocarp sloughing off, fruit beak and body splitting longitudinally. Right: fruit with exocarp gone and longitudinal splitting completed.

The shape and center of gravity of the dehisced fruits are such that these fruits usually lie with the distal or median portion of the lower surface of the body in contact with the ground, with the proximal portion somewhat elevated, and with the "horns" pointing upward (see Figure 3). This position is the one in which the fruit is most likely to hook onto the feet or ankles of animals, including students of floral biology. Many times I have had to remove *Proboscidea* fruits that had hooked onto my stockings. One of my students at the Biological Station, mentioning that an Oklahoma name for *Proboscidea* is "cow catcher," told me that one of her minor chores, as a child on a farm, was periodically to gather and remove from the barn floor the unicorn plant fruits that stock had brought in. Presumably — although I did not personally observe this — seeds are scattered from the fruits as animals carry them about. The seeds, large and black, are 7 - 10 mm long. The number of seeds per fruit, in the 10 fruits whose seeds I counted, ranged from 15 to 67.

ACKNOWLEDGEMENTS

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REVISION OF VERNONIA (COMPOSITAE), SUBSECTION PANICULATAE, SERIES UMBELLIFORMES OF THE MEXICAN HIGHLANDS

Samuel B. Jones, Jr.

Vernonia is a large genus of 800 to 1,000 species, particularly abundant in South America, in certain regions of Africa, southeast Asia, and in North America (Willis, 1966). Although relatively uniform in its floral morphology, *Vernonia* exhibits extreme diversity in its vegetative features and includes herbs, shrubs, small trees, and vines. Because of the sheer number of taxa in *Vernonia* and lack of knowledge of most species, natural subdivisions of the genus have only rarely been fully circumscribed.

Subsection *Paniculatae* series *Umbelliformes* of section *Lepidapoa* established by Gleason (1906) seems to be an exception and appears to be a natural grouping. Gleason noted that the branches of the panicle are mostly aggregated or separated by shortened internodes, the peduncles are approximately uniform in length, the heads appear in subumbellate clusters which are in turn united into large pyramidal or hemispheric inflorescences. The plants are herbaceous to suffruticose perennials. The 10 species appear closely related and all are found in the highland regions of Mexico.

Gleason (1906, 1922) recognized nine species and in this paper ten species and seven subspecies are treated with a greatly revised taxonomy. Keys, synonymies, descriptions, typifications, distribution maps and specimen citations are given for the taxa. A new species, *V. cronquistii,* is described from Guerrero and Oaxaca. *Vernonia liatroides* ssp. *gentryi* is described from Durango south to Jalisco. Several changes in rank are made: *V. inuloides* is reduced to *V. karvinskiana* ssp. *inuloides; V. ehrenbergiana* is treated as *V. liatroides* ssp. *ehrenbergiana;* and *V. vernonioides* is now *V. seratuloides* ssp. *vernonioides.*

During the past four years, six of the 10 species have been studied in the field and in the greenhouse. Chromosome numbers, sesquiterpene lactones, and flavonoids have been determined for some of the taxa and hybridization experiments have been carried out within the group and with certain other Vernonias. The cytogenetical and phytochemical data provided considerable information and insight into the systematics of the group and they are presently being prepared for separate publication and will only be briefly summarized here.

Vernonia alamanii, V. serratuloides, and the three subspecies of *V. liatroides* have the sesquiterpene lactone Glaucolide-A (Mabry, et al., 1975). This bitter compound is found in 10 species of the closely related subsection *Paniculatae* series *Verae* from eastern North America; it is found as well in several species from South America. The flavonoid chemistry of *V. alamanii* and *V. liatroides* is similar also to that of series *Verae* with one exception; a compound tentatively identified as 3, 3′ -0- dicayl quercetin 7-0-glucoside is present in the series *Umbelliformes* but not in series *Verae* (Mabry, et al., 1975).

Seven of the 10 species are known chromosomally, each having $n = 17$, the same as the 18 species of series *Verae* from eastern North America (Jones, 1974). Experimental hybridizations within and among our accessions of series *Umbelliformes* generally have yielded fertile F_1 hybrids, but crosses between members of series *Umbelliformes* and series *Verae* have yielded vigorous but sterile F_1 hybrids. The phytochemical and cytogenetical data, briefly summarized here, support Gleason's (1923) conclusions that these two series were derived from a common ancestral line.

The taxonomic treatment presented here represents a synthesis of the results of various systematic techniques, but the descriptive and revisionary aspects have been largely drawn from about 900 herbarium specimens borrowed from BM, DUKE, ENCB, F, GA, GH, K, LD, MEX, MINN, MO, NY, P, TEX, UC, UMO, and US.

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KEY TO THE SPECIES

1. Peduncles multi-bracteate throughout with short bracts 1-2 mm long, similar to the outer phyllaries; heads 3-5 flowered; outer phyllaries glandular-tomentose; rare and local from the state of Tepic. .... 10. *V. feddemae*
1. Peduncles not bracteate or with only one or two bracts over 2 mm long, not similar to the outer phyllaries; heads (4) 5 or more flowered; outer phyllaries glabrate to glandular or slightly pubescent.
    2. Involucre height 13-24 mm, width 11-18 mm. .... 1. *V. alamanii*
    2. Involucre height 4-12 (15) mm, width 3-12 mm (14).
        3. Achenes pilose to pilose-hispid or ciliate on the ribs.
            4. Heads with over 50 flowers. .. 9. *V. barclayi*
            4. Heads with less than 20 flowers.
                5. Heads (4) 5-6 (7) flowered; leaf blades 20-30 cm long, 6-15 cm wide; inner phyllaries acuminate. ...... 7. *V. autumnalis*
                5. Heads 10-14 (18) flowered; leaf blades 6-14 (16) cm long, 2-9 cm wide; inner phyllaries acute to cuspidate.

6. Leaf blades tomentose to hirsute-villous beneath; distributed from Oaxaca to Chiapas. .... 5. *V. oaxacana*
6. Leaf blades glabrate beneath; distributed from Guerrero to Oaxaca. .... 4. *V. cronquistii*

3. Achenes glabrate to glandular or resinous-glandular.
   7. Outer phyllaries long-acuminate terminating gradually in a sharp point, (2) 3-6 mm long, tips 1-3 mm long. .... 8. *V. bealliae*
   7. Outer phyllaries acute, acute-acuminate, or apiculate to bitten, not terminating gradually into a sharp point, 0.8-2.5 mm long, tips less than 1.5 mm long.
      8. Heads 20-60 (70) flowered; inner phyllaries emarginate with mucro in notch, often bitten, sometimes acute-acuminate. .... 2. *V. karvinskiana*
      8. Heads 8-20 (25) flowered; inner phyllaries acute, sometimes slightly apiculate, or mucronate.
         9. Leaf blades 2-14 cm wide, ovate-lanceolate to lanceolate, length/width ratio 2-3. .... 3. *V. liatroides*
         9. Leaf blades 1-3 cm wide, oblong to linear-lanceolate, length/width ratio (2.2) 3-8. .... 6. *V. serratuloides*

1. **Vernonia alamanii** DC. Prodr. 5: 61. 1836. TYPE: México: *Alaman* 1831 (Holotype: G-DC, as photo F! US! as IDC microfiche G-DC!).

Cacalia alamanii (DC.) Kuntze, Rev. Gen. Pl. 2: 969. 1891.

Vernonia dictyophlebia Gleas. Bull. New York Bot. Gard. 4: 203. 1906. TYPE: México: Michoacán: Hills of Patzcuaro, *Pringle* 3347 (Holotype: NY! Isotypes: BM! ENCB! F! GH! K! MEX! MINN! MO! NY! P! UC! US!).

Vernonia alamanii DC. var *dictyophlebia* (Gleas.) McVaugh, Contrib. Univ. Michigan Herb. 9: 477. 1972.

Suffruticose, 1-2 m tall; stems floccose, becoming glabrate below. Leaves cauline; leaf blades 8-14 cm long, 3.5-7 cm wide (length/width ratio ca. 2.2), widest below the middle, ovate, ovate-lanceolate, to lanceolate, scabrous above, veiny and either glabrous or pilose-hispid below, apically acute, basally cuneate, margins serrate; petioles 7-33 mm long, floccose. Inflorescences hemispheric or depressed, variable in size. Heads (43) 51-65 (76) flowered; peduncles 2-4 cm long, floccose, aggregated into clusters. Involucres campanulate, 13-24 mm high, 11-18 mm wide; phyllaries glabrous, margins fimbriate, loosely imbricated, outer reflexed, greenish to brownish-purple; inner phyllaries linear to linear-spatulate, 11-19 mm long, 1.5-4 mm wide, tips mucronate-aristate, mucro 0.3-3.5 mm long; outer phyllaries linear to lanceolate or ovate, 4.5-9 (11) mm long, 1.5-3.2 (4) mm wide. Pappus straw-colored; inner bristles (6) 7-11 mm long, outer bristles 0.8-1.7 mm long. Corollas (9.6) 12-19 (21) mm long, reddish-purple. Anthers 3-5 (6.1) mm long. Achenes 3-4.5 mm long, densely white glandular, ca. 10 ribbed, basally terminating in a prominent yellow areola. Chromosome number $n = 17$. Flowering and fruiting occur from November to February (April).

This species is distributed from San Luis Potosí to Jalisco, Michoacán, and Guerrero as shown in Fig. 1. It grows on rocky limestone or volcanic hillsides, fields and roadsides in the oak-pine zone from ca. 1,800 to 2,600 m altitude. This species is centered on the Neo Volcanic Plateau and extends southward into the Sierra Madre del Sur and northward into the Sierra Madre Oriental. Gleason recognized two species but as McVaugh (1972) pointed out, they are not separable on the basis of lower leaf surface. McVaugh's use of the length of the phyllary awns breaks down when one examines a large sample of specimens. The specimens from Michoacán tend to have broader and more pubescent leaves but even this is highly variable.

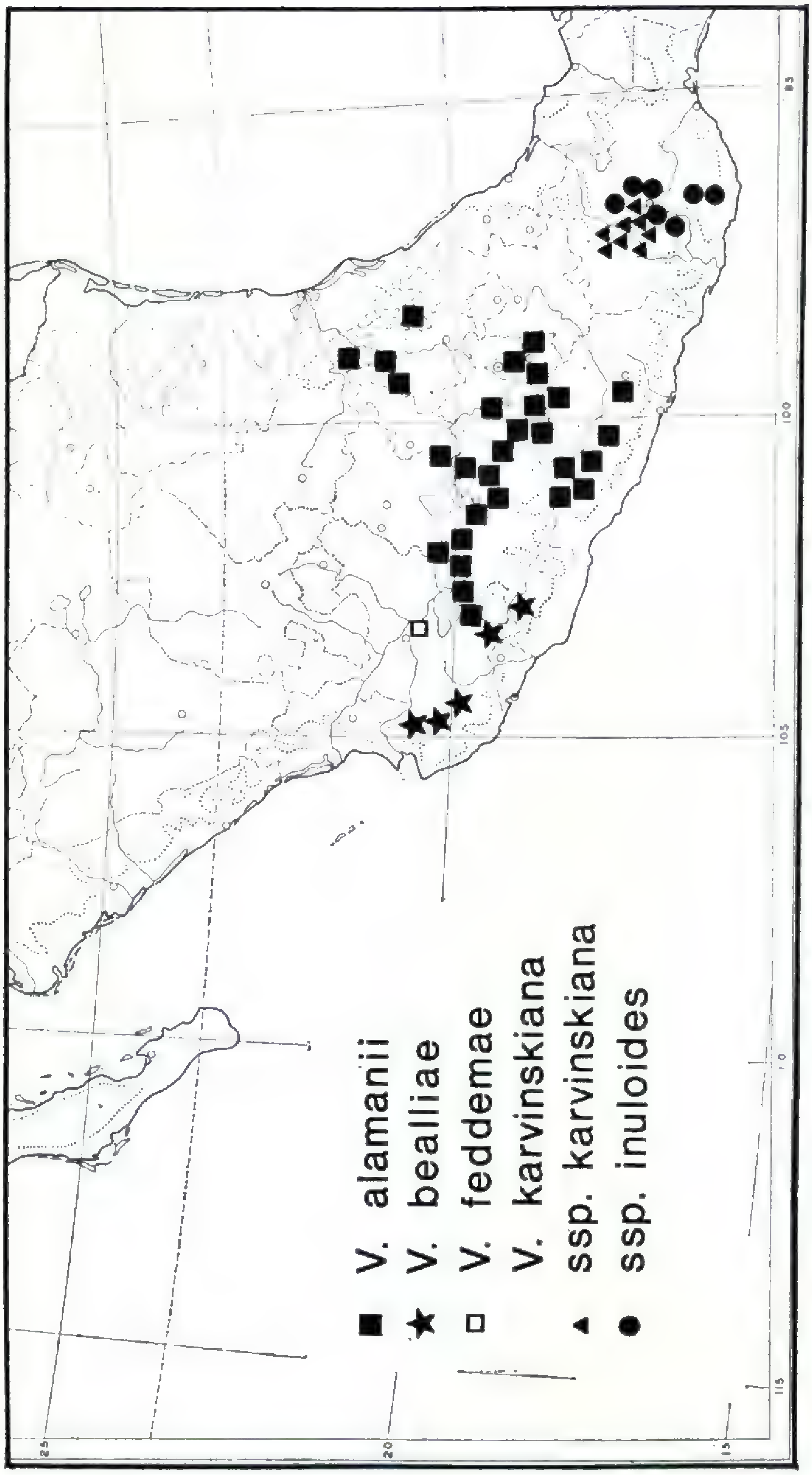


Fig. 1. Distribution of *Vernonia alamanii*, *V. bealliae*, *V. feddemae* and *V. karvinskiana*.

REPRESENTATIVE SPECIMENS: México: San Luis Potosí: ca. 10 mi W Xilitla, hwy 120, *King* 4438 (F, MICH, TEX, UC, US); Hidalgo: 9 mi NE Jacala, hwy 85, *King* 4216 (F, MICH, TEX, UC, US); Veracruz: Huayacocotla, *R. Hdez M. & Vazquez de Hdez* 986 (GH); Guanajuato: Acámbaro, *Rzedowski* 25349 (MICH); Jalisco: Mazamita, *Díaz Luna* 3164 (ENCB); Michoacán: Zitacuraro-Zirahuato, *Hinton* 13541 (GH, MICH, TEX, UC); México: Temascaltepec, *Hinton* 8881 (MICH, TEX, UC, US); DF: Canada of Contreas, *Pringle* 15034 (F, MICH, MIN, MO, TEX); Morelos: Mountain side above Cuernavaca, *Pringle* 8045 (F, GH, MEX, MICH, MIN, UC); Guerrero: San Antonio-Buenos Aires, Montes de Oca, *Hinton* 14071 (GH, MICH, TEX, UC, US).

Natural hybridization occasionally occurs between *Vernonia alamanii* and *V. liatroides* ssp. *ehrenbergiana*. Hybrid specimens examined include: México: México: Pineda, Temascaltepec, *Hinton* 3187 (NY, GH); Nanchititla, Temascaltepec, *Hinton* 7546 (K, US); Michoacán: 12 mi NW of Morelia on hwy 15, *Jones* 20574 (GA).

One putative hybrid between *V. alamanii* and *V. liatroides* ssp. *liatroides* was collected: México: Hidalgo: 0.3 mi N km 150 hwy 85, 11 mi S of State Line, *Chapman* 63 (GA).

2. **Vernonia karvinskiana** DC. Prodr. 5: 62. 1836. TYPE: México: *Karwinski s.n.* (Holotype: G-DC, as IDC microfiche G-DC!; isotypes: P! M, as photo NY! US!).

Ascending, suffruticose perennial, 1-3 m in height; stems glabrate to hispid or floccose. Leaves cauline; upper leaf blades (4.5) 6-10 (11.5) cm long, (0.5) 2-5 (6) cm wide (length/width ratio ca. 2-3), widest at or below the middle, lanceolate to ovate, scabrous above, glabrate to floccose below, apically acute to acuminate, basally cuneate or sometimes rounded-truncate, margins serrate to almost entire; petioles 2-11 mm long, hispid to glabrate or floccose. Inflorescences pyramidal, variable in size but often 1 dm across. Heads 20-60 (70) flowered; peduncles 1-3 cm long, glabrate or pilose to floccose, subumbellate. Involucres vase-shaped, (7) 8-13 (15) mm high, 6-12 (14) mm wide; phyllaries glabrous to resinous, loosely appressed, dark purple to greenish; inner phyllaries lanceolate to linear-

oblong, (6) 7-11 (12) mm long, 1.3-2.6 mm wide, tips emarginate with a mucro in the notch, sometimes bitten or apiculate; outer phyllaries lanceolate, 2.2-6 mm long, 0.7-2.5 mm wide. Pappus straw-colored; inner bristles 5.2-7 mm long, outer bristles 0.5-2 mm long. Corollas (8) 9-12 (13.5) mm long, reddish-purple. Anthers 2.8-4.5 (5) mm long. Achenes 3-4.3 mm long, furrows often glandular, ca. 9 or 10 ribbed. Chromosome number $n = 17$. Flowering and fruiting occur from Sept. to Feb. (Mar.).

This species is restricted to the state of Oaxaca. It grows on rocky hillsides, moist mountain slopes, ridges, or disturbed grassy areas in full sun or partial shade of oak or pine-oak woodlands at an altitude of 1700-2100 m.

Two subspecies are recognized. Their distributions are shown in Fig. 1. They may be characterized and distinguished by the following key:

Inner phyllary tips usually acute; flowers per head 20-30 (34). .... 2a. ssp. *karvinskiana*

Inner phyllary tips usually truncate; flowers per head (30) 35-60 (70). .... 2b. ssp. *inuloides*

2a. **Vernonia karvinskiana** DC. ssp. **karvinskiana.**

Vernonia corymbiformis DC. Prodr. 5: 62. 1836. TYPE: México: *Karwinski s.n.* (Holotype: G-DC, as IDC microfiche G-DC! Isotypes: P! M, as photo NY! US!). (not Gleas. Bull. New York Bot. Gard. 4: 198. 1906).

Cacalia karvinskiana (DC.) Kuntze, Rev. Gen. Pl. 2: 970. 1891.

Cacalia corymbiformis (DC.) Kuntze, Rev. Gen. Pl. 2: 969. 1891.

Vernonia conzattii Robins. Proc. Amer. Acad. 44: 615. 1909. TYPE: México: Oaxaca: Sta. Ines del Monte, Zimatlan, *Conzatti* 1327 (Holotype: GH! Isotype: MEX!).

This subspecies is common in the oak woodlands of the Sierra Madre de Oaxaca. It intergrades with ssp. *inuloides* in the Altiplano de Oaxaca.

REPRESENTATIVE SPECIMENS: México: Oaxaca: Amongst dwarf oaks, dry hills above Las Sedas, 7,000 ft., *Pringle* 6019 (GH, MEX, MICH, MIN, MO, NY, P, UC, US); in oak woodland at summit about 15 km N of Telixtlahuaca on road to Tehuacan, Elev. 2100 m, *Cronquist & Fay* 10914 (NY, TEX, US).

2b. **Vernonia karvinskiana** ssp. **inuloides** (DC.) S. B. Jones, stat. nov.

Vernonia inuloides DC. Prodr. 5: 62. 1836. TYPE: México: *Karwinski s.n.* (Holotype: G-DC, as IDC microfiche G-DC!, as photo NY! US! Isotype: P!).

Cacalia inuloides (DC.) Kuntze, Rev. Gen. Pl. 2: 970. 1891.

This subspecies is common in the oak-pine woodlands of the Altiplano de Coatlan and the Altiplano de Mixtepec northward into the Altiplano de Oaxaca.

REPRESENTATIVE SPECIMENS: México: Oaxaca: 12 miles S of Sola de Vega and 90 miles N of Puerto Escondido, *Cronquist & Sousa* 10504 (GH, MEX, MICH, NY, TEX); 80 miles S of Oaxaca, S of Miahuatlán, *Cronquist & Sousa* 10445 (GH, MEX, MICH, NY).

A splitter perhaps would have recognized two species; however the differences between these two taxa are more apparent than real. Sixteen morphological features were measured or scored on 25 herbarium specimens of each taxon; most were not useful as key characters. The most distinctive features are compared in Fig. 2 where their overlap is readily apparent. The morphological variation of the two subspecies was undoubtedly reinforced by their geographical isolation. Subspecies *karvinskiana* occurs in the mountains to the north of the city of Oaxaca and ssp. *inuloides* is centered in the mountains south of there; in between they intergrade completely. The close relationship of these two taxa is best shown by treatment at the rank of subspecies. If treated as two distinct species this relationship is likely to be obscured.

3. **Vernonia liatroides** DC. Prodr. 5: 34. 1836. TYPE: México: Tamaulipas: Tula to Tampico, *Berlandier* 2139 (Holotype: G-DC, as IDC microfiche G-DC! as photograph US! Isotypes: GH! NY! P!).

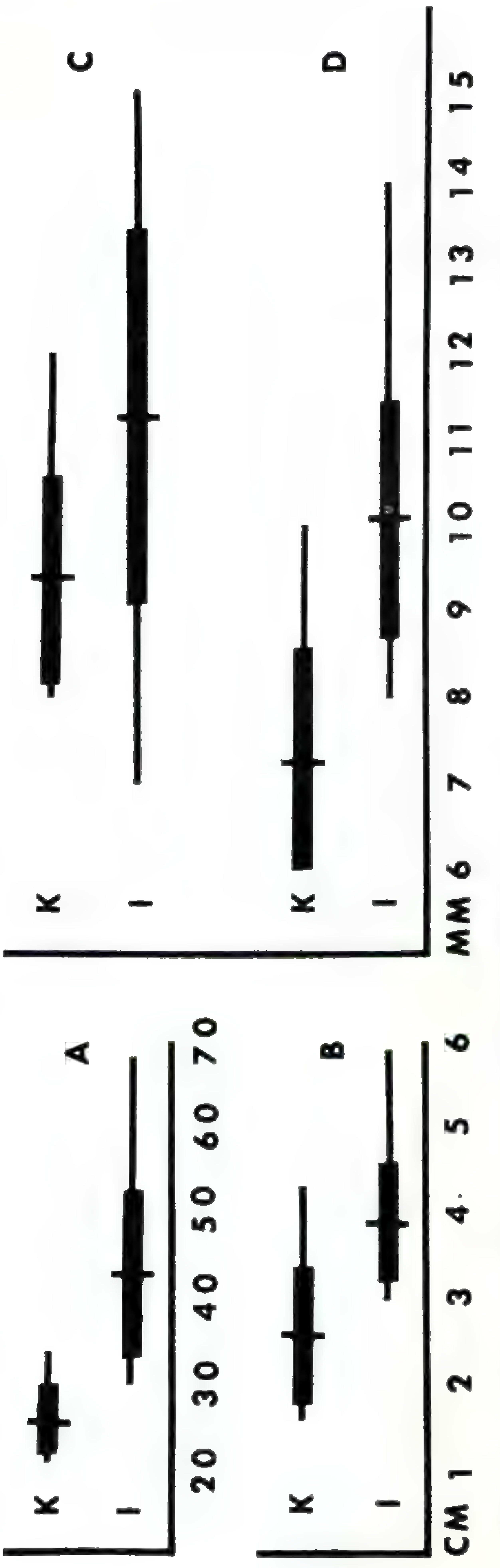


Fig. 2. Ranges, means, and standard deviations of characters of *Vernonia karvinskiana* ssp. *karvinskiana* (K) and ssp. *inuloides* (I). A, number of flowers per head; B, width of the leaf blade; C, height of the involucre; D, width of the involucre.

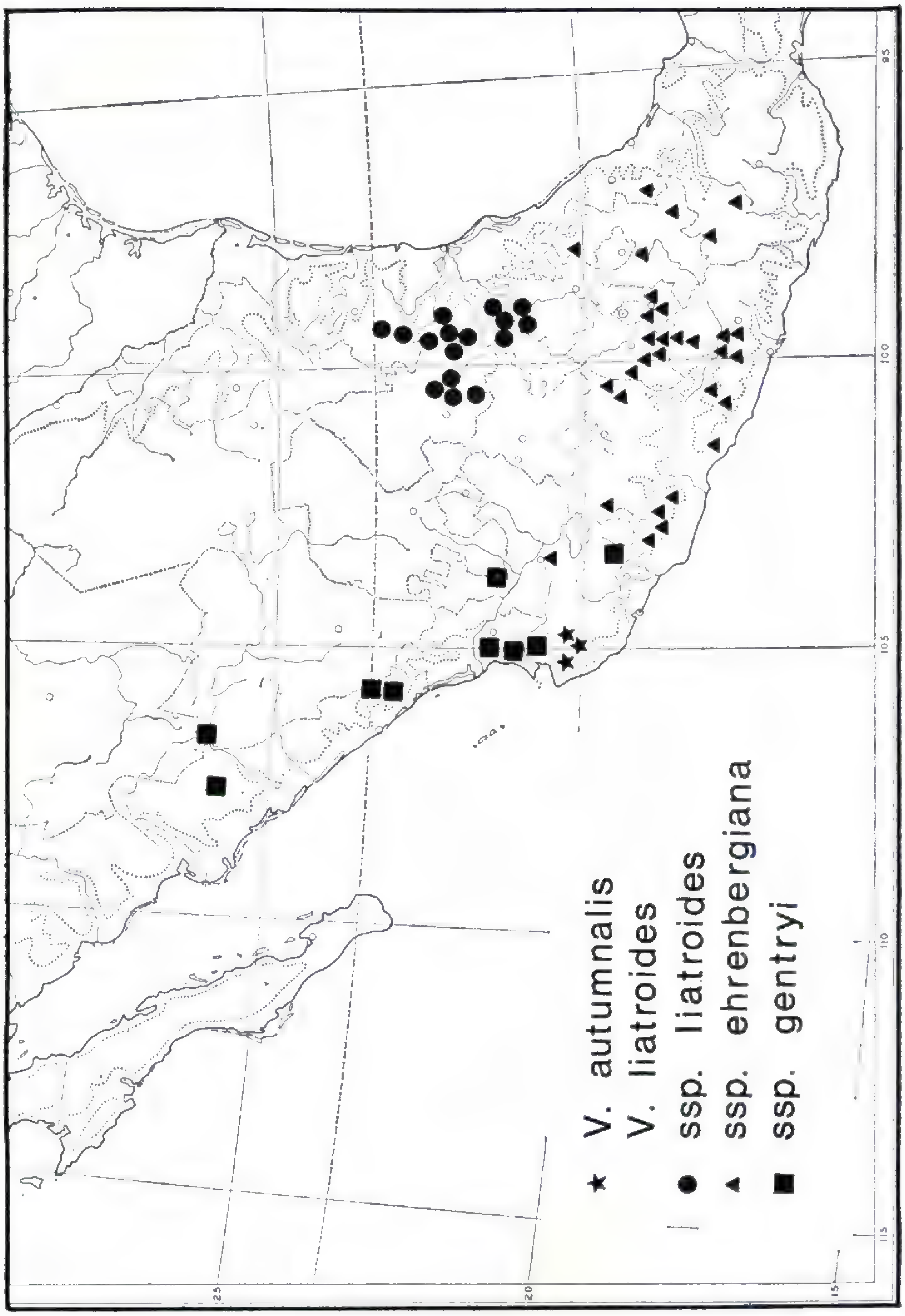
Herbaceous perennial, sometimes becoming frutescent, 1-3 m; stems pilose-hispid or sometimes glabrate. Leaves cauline; leaf blades 4.5-25 cm long, 2-14 cm wide (length/width ratio ca. 2-3), widest at the middle, lanceolate or ovate-lanceolate, slightly scabrous or almost glabrate above, punctate, pilose-hispid, or glabrate below, apically acute, basally cuneate, margins serrate; petioles 0.4 to 3.5 cm long, downy to glabrate. Inflorescences narrowly pyramidal to broadly pyramidal. Heads (8) 9-20 (25) flowered; peduncles 3-5 mm long, downy to glabrate, subumbellate. Involucres campanulate, (3.7) 4.5-6.5 (8) mm high, (2.8) 4-6 (7.5) mm wide; phyllaries ciliate, loosely appressed, greenish-purple sometimes shiny; inner phyllaries oblong-lanceolate, (3.2) 4-5 (6) mm long, (0.8) 1-1.5 (1.7) mm wide, tips acute, slightly apiculate; outer phyllaries lanceolate, (0.8) 1.3-2.3 (2.5) mm long, 0.5-1.2 (1.8) mm wide. Pappus whitish; inner bristles 4.5-6.4 mm long, outer bristles 0.8-1.5 mm long. Corollas (5) 6-10 (11) mm long, reddish-purple to light pink, fading to almost white, glabrous, very fragrant. Anthers 2-4 mm long. Achenes 2-3.2 mm long, resinous glandular or sometimes glabrous, ca 10 ribs. Chromosome number $n = 17$. Flowering and fruiting occur from October to May.

This species is distributed from the Sierra Madre Oriental south and west across the Neo Volcanic Plateau and northward along the Sierra Madre del Sur and the Buried Ranges and Sierra Madre Occidental.

Three subspecies are recognized. Their distributions are shown in Fig. 3. They may be characterized and distinguished by the following key:

Plants normally flowering from October to December, from the Sierra Madre Oriental, or the Neo Volcanic Plateau and the Sierra Madre del Sur; leaf blades (4) 5-11 (13) cm long, 2-5 (7) cm wide, petioles 0.3-1.3 cm long; flowers per head (8) 9-13 (17).

Fig. 3. Distribution of *Vernonia autumnalis* and *V. liatroides*.


V. autumnalis
V. liatroides
ssp. liatroides
ssp. ehrenbergiana
ssp. gentryi

Plants from the Sierra Madre Oriental, frutescent herbaceous perennial; corolla lobes (2.2) 2.5-3.5 (4.2) mm long, corolla (5.5) 7-9 mm long. . 3a. ssp. *liatroides*

Plants from the Neo Volcanic Plateau and the Sierra Madre del Sur, herbaceous perennial; corolla lobes 1.8-2.2 (2.7) mm long, corolla 5-7.5 mm long. .... 3b. ssp. *ehrenbergiana*

Plants normally flowering from late February to April, from the Buried Ranges and the Sierra Madre Occidental; leaf blades (9) 11-20 (25) cm long, (4) 5-11 (15) cm wide, petioles 0.8-3.5 cm long; flowers per head (11) 12-19 (25). .... 3c. ssp. *gentryi*

3a. **Vernonia liatroides** ssp. **liatroides.**

Eupatorium tulanum Klatt, Abh. Nat. Ges. (Halle) **15:** 323. 1882. TYPE: México: Tamaulipas: Tula to Tampico, *Berlandier* 2139 (Holotype GH! Isotypes: G-DC, as IDC microfiche G-DC! P!).

Cacalia liatroides (DC.) Kuntze, Rev. Gen. Pl. **2:** 971. 1891.

This subspecies is common on limestone hillsides, in mesic habitats of the Sierra Madre Oriental in the tropical deciduous forest up and into the pine-oak zone. Flowering and fruiting normally occur from October to January. The plants become woody near the base of the stems.

REPRESENTATIVE SPECIMENS: México: Tamaulipas: *Viereck s.n.* (US); San Luis Potosí: 19 mi WSW Xilitla, hwy 120, oak-pine forest, red limestone soil, *Jones* 22376 (GA); Hidalgo: 27 mi S Tamazunchale at Santa Maria, shrub 2 m. tall, rocky hillside, *Jones* 20560 (GA); Queretaro: 5 mi WSW Jalpan, hwy 120, abundant along limestone roadsides, *Jones* 22378 (GA).

3b. **Vernonia liatroides** ssp. **ehrenbergiana** (Sch. Bip.) S. B. Jones, stat. nov.

Vernonia ehrenbergiana Sch. Bip. Linnaea **20:** 513. 1847. TYPE: México: Barranco pr. los reyes, *Ehrenberg* 710 (Holotype P!).

Cacalia ehrenbergiana (Sch. Bip.) Kuntze, Rev. Gen. Pl. 2: 971: 1891.

Vernonia capreaefolia Gleas. Bull. N.Y. Bot. Gard. 4: 200. 1906. TYPE: México: Veracruz: Orizaba, *Schaffner* 117 (Holotype: GH!).

This subspecies is commonly found along roadsides and on rocky hillsides in the Neo Volcanic Plateau and the Sierra Madre del Sur. In the latter region it is often associated with limestone. It appears to be a herbaceous perennial, unlike the other two subspecies which become suffrutescent. Subspecies *ehrenbergiana* and ssp. *gentryi* intergrade in western Jalisco. Flowering and fruiting occur from October to January.

REPRESENTATIVE SPECIMENS: México: Jalisco: Guadalajara, *Pringle* 2943 (GH); Michoacán: km 115 hwy 15 between Zitacuaro and Cd. Hidalgo, *Jones* 20572 (GA); Guerrero: 8 km SW Xochipala, *Feddema* 2765 (ENCB, MICH, TEX); México: 2 mi N Ixtapan de Sal hwy 55, *Jones* 20569 (GA); Oaxaca: Huajuapam, *Nelson* 1979 (GH, US); Puebla: by streams near Tehuacan, *Pringle* 6246 (BM, ENCB, F, GH, MEX, MIN, P, UC, US); Veracruz: Orizaba; *Bourgeau* 3339 (F, GH, K, US).

3c. **Vernonia liatroides** ssp. **gentryi** S. B. Jones, ssp. nov. TYPE: México: Durango: 116 mi W of Durango on hwy 40, elev. 2000 m, *Jones* 22527 (Holotype: GA!).

Folia 10-25 cm longa, 5-15 cm lata (ratione longitudinis cum latitudine 1.5-2.5), ovali-lanceolata, vel lanceolata. Capitula (11) 13-18 (25) flora.

This subspecies is abundant at elevations of ca 1,500 to 2,000 m on the mesic west slopes in the pine-oak zone down into the tropical deciduous forests of the Buried Ranges and the Sierra Madre Occidental. It is named in honor of Howard Scott Gentry, whose collections from northwest Mexico have facilitated my studies of this and other species of *Vernonia*. Flowering and fruiting occur from March to May.

REPRESENTATIVE SPECIMENS: México: Durango: San Ramón, *Palmer* 140 (F, GH, MO, NY, US); Sinaloa: 132 mi W Durango near El Batel on hwy 40, *Jones* 22528 (GA); Nayarit: 15 km W Tepic, sobre el camino a Jalcocotán, *Rzedowski* 15614 (ENCB, MEX, MICH). Jalisco: San Sebastian, Hacienda del Ototal, *Mexia* 1681 (BM, F, GH, MICH, MIN, MO, NY, UC, US); Zacatecas: 5 mi SW Mezquital del Oro, *McVaugh* 22135 (ENCB, MICH, NY).

Nineteen morphological features were measured on 25 specimens of each of the three taxa. The measurements in general showed considerable overlap; however, those presented in Fig. 4 are of some diagnostic value. Keeping in mind the many features shared by these three taxa, they are best treated as subspecies.

4. **Vernonia cronquistii** S. B. Jones, sp. nov. TYPE: México: Guerrero: semi-open slopes in pine-oak forest in the mountains along the highway ca. 62 rd miles N of Acapulco, and 20 mi S of Chilpancingo, *Cronquist* 9705 (Holotype: NY! Isotypes: GH! MEX! MICH! MO! NY!).

Herba perennis, erecta, 1.5-metralis; caules purpurei necnon glabri. Folia caulina (6.5) 8-12 (15) cm longa, 1.9-4.5 cm lata (ratione longitudinis cum latitudine ca. 3-4), ad medium dilatata, ovato-lanceolata, supra scabridiuscula, infra glabrescentia, apicibus acuminatis, basibus anguste cuneatis, marginibus serratis; petioli 0.5-1.2 cm longi glabrescentes. Inflorescentiae paniculatae-umbellatae. Capitula 10-14(18)-flora, cum pedunculis 0.5-1.3 cm longis. Involucra anguste campanulata 5.5-8.5 mm longa, 3-7.5 mm lata; phyllaria ciliata, laxe imbricata, purpurea, eis interioribus lineari-lanceolatis, 4.2-7.5 mm longis, 0.9-1.5 mm latis, apicibus acutis vel cuspidatis, eis exterioribus lanceolatis, 1-2 mm longis, 0.6-0.9 mm latis. Pappi setae albae, eis interioribus 5-6.1 mm longis, eis exterioribus 0.6-1.1 mm longis. Corollae (7.3) 9-11 (12.6) mm longae, Vernonia-purpureae, glabrae. Antherae 2.7-3.3 mm longae. Achaenia 2.2-3.1 mm longa, piloso-hispida, ca. 9-11 nervata. Chromosome number $n = 17$. Flowering and fruiting occur from October to December. This species is dis-

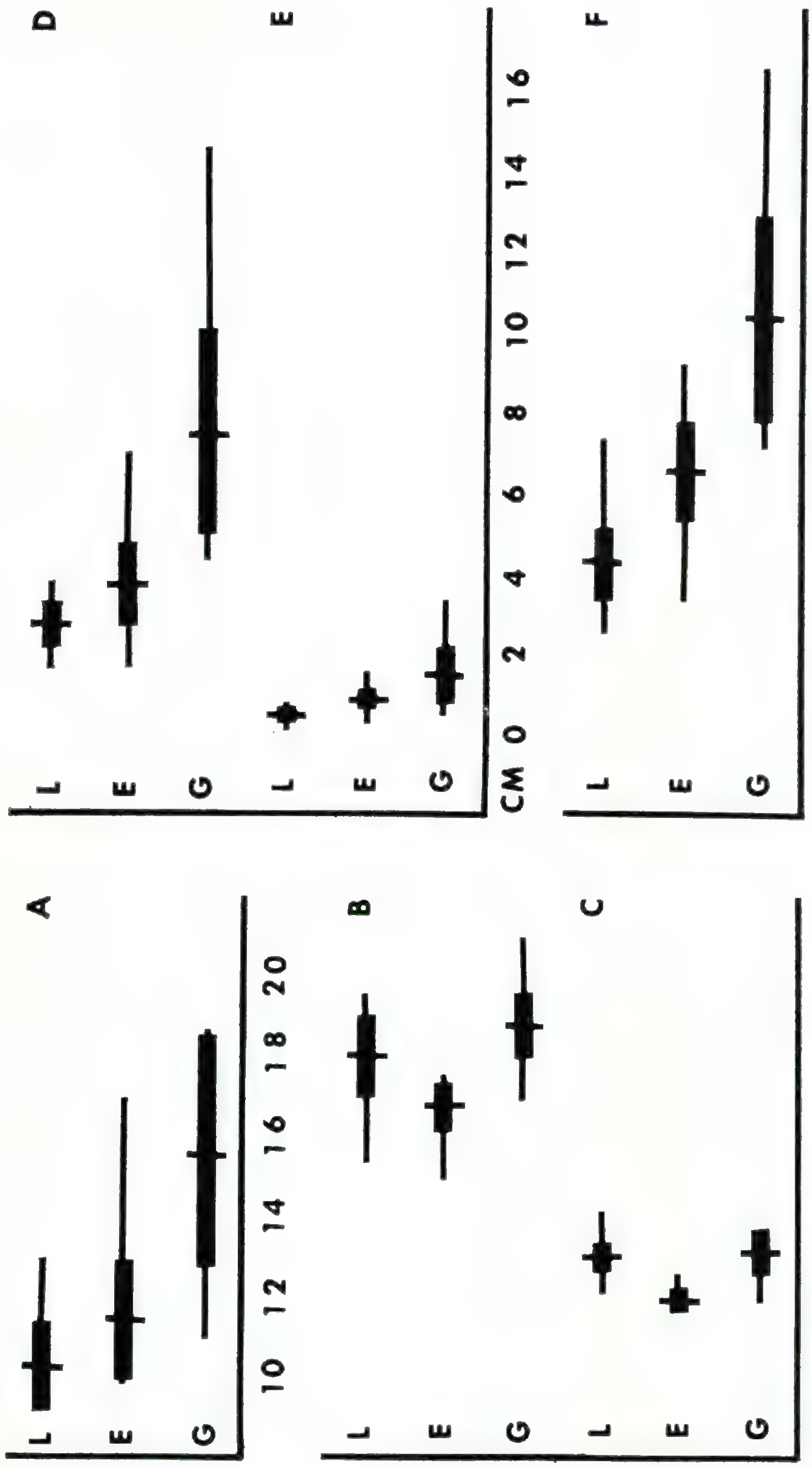


Fig. 4. Ranges, means, and standard deviations of characters of *Vernonia liatroides* ssp. *liatroides* (L); ssp. *gentryi* (G); ssp. *ehrenbergiana* (E); A, number of flowers per head; B, length of the corolla; C, length of the lobes of the corolla; D, width of the leaf blade; E, length of the petiole; F, length of the leaf blade.

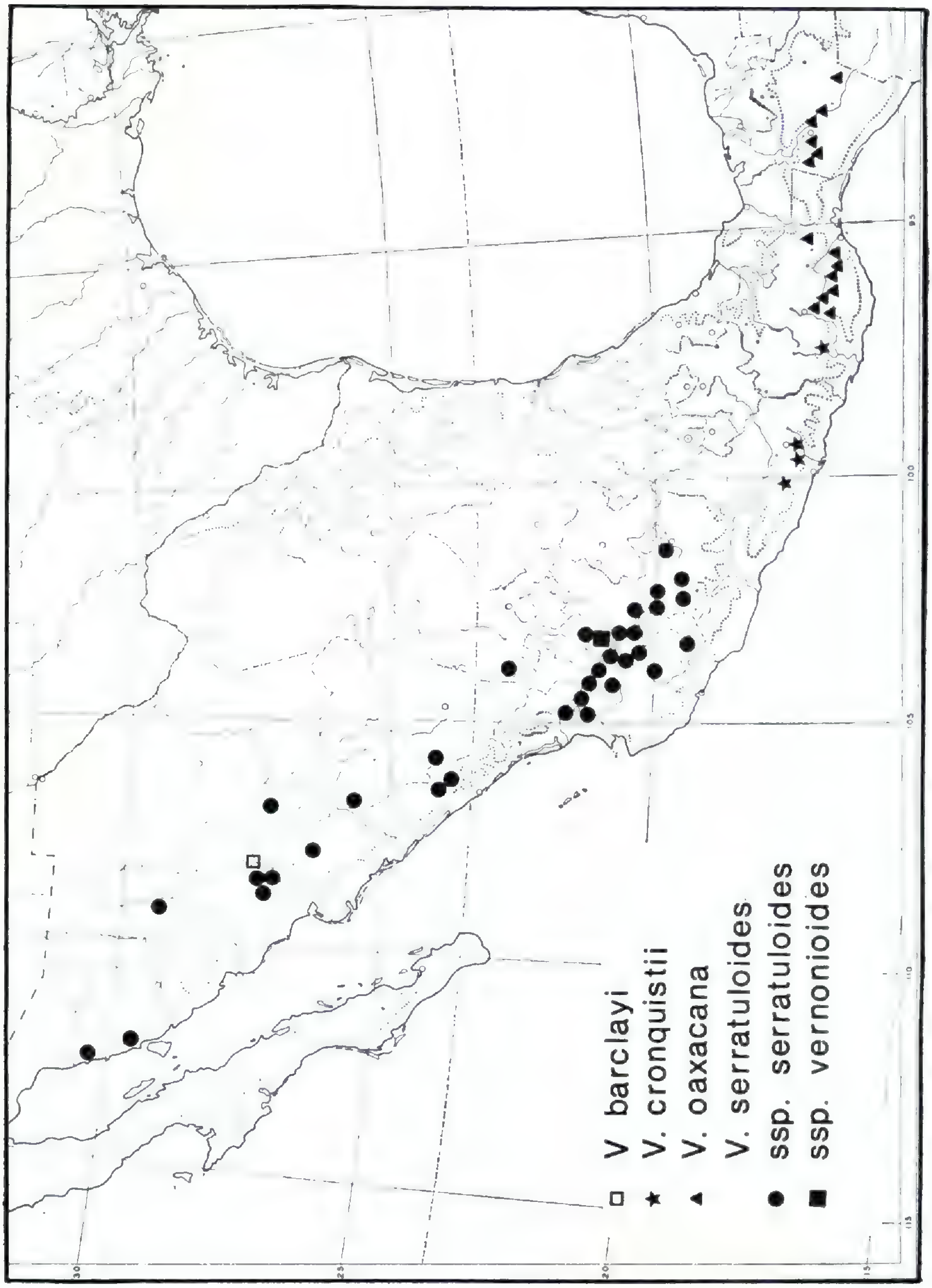
tributed from Guerrero to Oaxaca along the Sierra Madre del Sur as shown in Fig. 5. It occurs on semi-open slopes in pine-oak or pine forests at elevations of 700-950 m. It is named in honor of Dr. Arthur Cronquist who made the type collection and has provided encouragement to me with my studies of *Vernonia*.

Additional specimens examined include: México: Guerrero: Rincón de la Via, *Kruse* 739 (ENCB); Plan de Carrizo, Galeana, *Hinton* 11035 (GH, K, MICH, NY, US); Oaxaca: 5-6 km NE Putla rd to Tlaxiaco, *McVaugh* 22273 (ENCB, MICH).

5. **Vernonia oaxacana** Sch. Bip. ex Klatt, Leopoldina **20**: 74. 1894. TYPE: México: Chiapas: San Carlos, *Liebmann* 49 (Syntypes: C, as IDC microfiche!, as photo and fragment US!, as photo F! NY! US!, as drawing and fragment GH!, as fragment P!).

Suffruticose, 0.5-2.5 m; stems hirsute-villous to tomentose, becoming glabrate with age. Leaves cauline; upper leaf blades 6.5-14 cm long, 2.4-8.7 cm wide (length/width ratio ca. 2), widest below the middle, elliptic-ovate, pilose-hispid above, tomentose to hirsute-villous below, apically acute, basally oblique to cuneate or rounded, margins serrate; petioles 0.7-2 cm long, villous. Inflorescences pyramidal, large, irregular, highly branched, with many leaves. Heads (10) 11-13 (15) flowered; peduncles 5-10 mm long, hispid, appearing subumbellate. Involucres campanulate, (5.3) 6-7 (8) mm high, 4.2-6.6 mm wide; phyllaries glabrous, loosely appressed, greenish purple; inner phyllaries oblong-lanceolate, 4.2-6.7 mm long, 0.8-1.5 mm wide, tips narrowly cuspidate; outer phyllaries lanceolate, 0.7-2.2 mm long, 0.3-1 mm wide. Pappus white; inner bristles 5-6.5 mm long, outer bristles 0.9-2.2 mm long. Corollas (7) 8-9 (10) mm long, reddish-purple. Anthers 2.5-3.5 mm long.

Fig. 5. Distribution of *Vernonia barclayi*, *V. cronquistii*, *V. oaxacana* and *V. serratuloides*.


V barclayi
V. cronquistii
V. oaxacana
V. serratuloides
ssp. serratuloides
ssp. vernonioides

Achenes 2-3.2 mm long, sparsely ciliate on ribs, rarely glandular, ca. 10 ribs. Chromosome number $n = 17$. Flowering and fruiting occur from Dec. to Feb.

This species is distributed from Oaxaca to Chiapas as shown in Fig. 5. This species grows in oak woodlands and on rocky roadsides at elevations of 900-1300 m.

REPRESENTATIVE SPECIMENS: México: Oaxaca: Along hwy 190, 67 mi W Tehuantepec, *King* 2476 (MICH, TEX, US); Chiapas: Roadside in low valley with palms, hwy 190, 15 mi S LaTrintaria, *Breedlove & Raven* 8433 (F, MICH).

6. **Vernonia serratuloides** H.B.K. Nov. Gen. Sp. 4: 33. 1818. TYPE: México: Michoacán: "Crescit regione temperata prope urbem Valladolid de Mechoacan, alt. 1000 hex." [Collector?] (Holotype: P, as photo F! as fragment P!).

Herbaceous perennial, ca. 1 m; stems glabrate to pilose-hispid or rarely downy. Leaves cauline, crowded; leaf blades (5.2) 6-12 (13.5) cm long, (0.8) 1-3 (3.8) cm wide (length/width ratio ca. 2.2-8), widest at or below the middle, oblong to linear-lanceolate, scabrous or sometimes glandular-punctate or glabrate above, glandular-punctate or scabrous to pilose-hispid below, apically acute, basally cuneate, margins remotely toothed; petioles 2-5 mm, glabrate to pilose-hispid. Inflorescences narrowly pyramidal. Heads 9-19 flowered; peduncles 3-8 mm long, pilose-hispid to almost downy, subumbellate. Involucres narrowly campanulate, 6-9 mm high, (4) 4.5-9 (10) mm wide; phyllaries ciliate or hirsute to almost glabrate on the margins, tightly appressed, greenish to purple; inner phyllaries oblong-lanceolate, 5-8 mm long, 1-1.5 mm wide, tips acute, sometimes with a small mucro; outer phyllaries lanceolate, 1.3-2.9 mm long, 0.5-1 mm wide. Pappus straw colored; inner bristles 5-6.5 mm long, outer bristles 0.4-1.2 mm long. Corollas 7.4-11 mm long, reddish-purple. Anthers 2.9-3.7 mm long. Achenes 2.5-3.3 mm long, glabrate to resinous-dotted, 9-11 ribs. Chromosome number $n = 17$. Flowering and fruiting occur from Sept. to Dec.

This species is distributed from Sonora southeastward into Jalisco and Michoacán as shown in Fig. 5. It grows on rocky hillsides, dry pastures, oak or oak-pine woodlands, fallow fields, often in sticky clay soil at altitudes of 300-1000 m. The range of this species is associated with the Sierra Madre Occidental and the northwestern part of the Neo Volcanic Plateau.

Two subspecies are recognized. They may be characterized and distinguished by the following key:

Leaf blade length/width ratio 4-8; flowers per head 9-14; corolla length 7.4-9 mm; involucre width 4-7 mm. .... 6a. ssp. *serratuloides*

Leaf blade length/width ratio 2.2-3.6; flowers per head 15-19; corolla length 9.1-11 mm; involucre width 6.5-10 mm. .... 6b. ssp. *vernonioides*

6a. **Vernonia serratuloides** ssp. **serratuloides.**

Vernonia sinclairi Benth. Bot. Voy. Sulph. 109. 1845. TYPE: México: Nayarit: San Blas-Tepic, *Sinclair s.n.* (Holotype K!).

Perezia paniculata Gray, Proc. Amer. Acad. Arts **21**: 393. 1886. TYPE: México: Chihuahua: Mountains above Batopilas at the Frailes, ca. 7,000 ft, *Palmer* 279 (Holotype: GH! Isotypes: BM! US!).

Cacalia serratuloides (H.B.K.) Kuntze, Rev. Gen. Pl. **2**: 970. 1891.

Cacalia sinclairi (Benth.) Kuntze, Rev. Gen. Pl. **2**: 970. 1891.

Vernonia umbellifera Gleas. Bull. New York Bot. Gard. **4**: 199. 1906. TYPE: México: Jalisco: Plains of Guadalajara, *Pringle* 2316 (Holotype: NY! Isotypes: BM! F! MEX! MO! NY! P! UC! US!).

Vernonia camporum M. E. Jones, Contrib. West. Bot. **18**: 69. 1933. TYPE: México: Jalisco: Orendain Nov. 27, 1930, *M. E. Jones s.n.* (Holotype: POM, as photo and fragment US!).

This subspecies is widespread with many collections from the southern part of its range. As to be expected there is some local variability but it is not sufficient to warrant recognition of additional taxa.

REPRESENTATIVE SPECIMENS: México: Sonora: Sierra de Alamos, *Gentry* 4862 (MICH, MO, NY, US); Chihuahua: rd. from Parral to Batopilas, *Goldman* 156 (US); Sinaloa: NW base of Cerro Colorado, *Gentry* 5192 (NY); Durango: Tamazula, *Ortega* 4443 (US); Nayarit: Laguna Santa Maria del Oro, *Windler* 2904 (MICH); Jalisco: Hills near Etzatlan, *Pringle* 11607 (F, MICH, MO, US); Michoacán: ca. 5 mi N Cotija and 22 mi S Jiquilpan, *King & Soderstrom* 4592 (MEX, MICH, NY, TEX, UC, US).

6b. **Vernonia serratuloides** ssp. **vernonioides** (Gray) S. B. Jones, stat. nov.

Perezia vernonioides Gray, Proc. Amer. Acad. Arts 22: 433. 1887. TYPE: México: Rio Blanco, in shady grassy bottoms, *Palmer* 745 (Holotype: GH!).

Vernonia vernonioides (Gray) Bacigal. Contr. Gray Herb. 97: 77. 1931.

Vernonia jaliscana Gleas. Bull. New York Bot. Gard. 4: 198. 1906. TYPE: México: Jalisco: Hills near Guadalajara, 5,000 ft., *Pringle* 9994 (Holotype: GH! Isotypes: F! MO! US!).

Subspecies *vernonioides* is known only from Jalisco near Guadalajara. The one exact location would place it in the dissected canyon country to the NNE of the city.

REPRESENTATIVE SPECIMENS: México: Jalisco: Ixtlahuacán de los Membrillos, oak woodland, *Detling* 8775 (MICH); Rocky hills near Guadalajara, *Pringle* 2884 (F, GH, MEX, NY).

Eighteen morphological features on all nine available specimens of ssp. *vernonioides* and on 25 specimens of ssp. *serratuloides* were measured or scored. The two subspecies share many morphological features indicative of a close relationship. They differ in few characters as shown in Fig. 6. The treatment of these two taxa places emphasis on their similarities rather than on their differences.

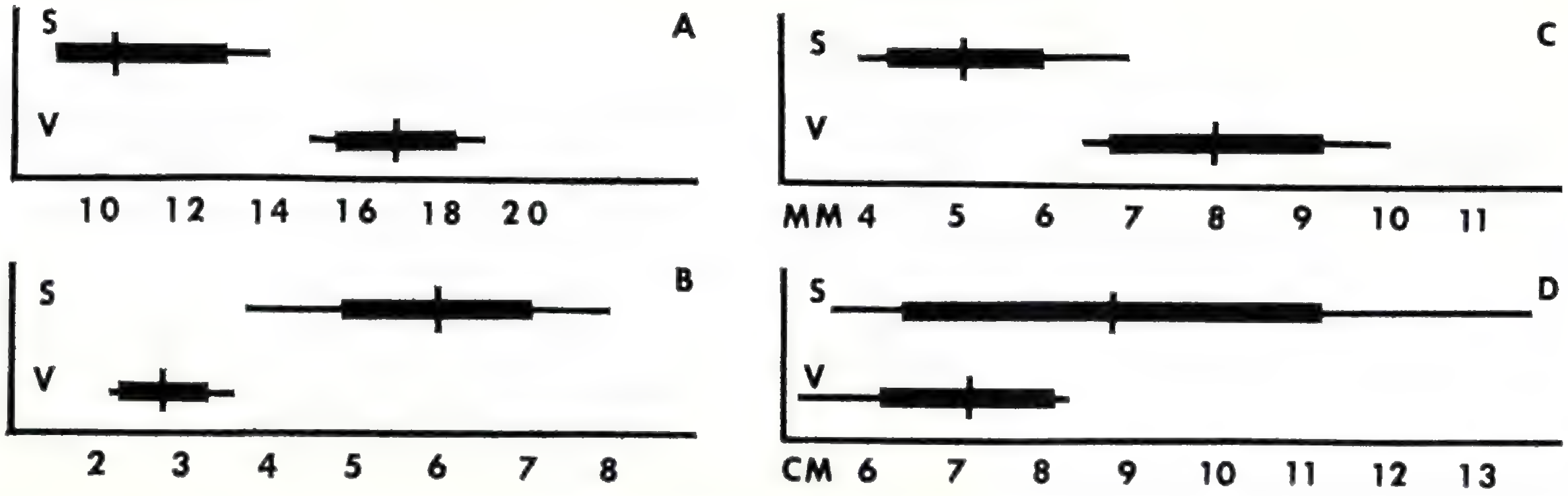


Fig. 6. Ranges, means, and standard deviations of characters of *Vernonia serratuloides* spp. *serratuloides* (S) and ssp. *vernonioides* (V). A, number of flowers per head; B, length/width ratio of the leaf blade; C, width of the involucre; D, length of the leaf blade.

7. **Vernonia autumnalis** McVaugh, Contr. Univ. Mich. Herb. 9: 477. 1972. TYPE: México: Jalisco: 5 km S. of La Huerta, in oak forest, elev. 500-550 m, *McVaugh* 19833 (Holotype: MICH. Isotype: GA!).

Herbaceous perennial, 1-2 m; stems lanate sometimes becoming glabrate, striate. Leaves cauline; leaf blades 20-30 cm long, 6-15 cm wide (length/width ratio ca. 2.5), widest at or above the middle, elliptic-oblanceolate, glabrous above, lightly resinous to arachnoid below, apically acute, basally cuneate, margins revolute and remotely toothed, sometimes pinnately 4-lobed; petioles 1-2.7 cm long, glabrate to lanate. Inflorescences broadly pyramidal. Heads (4) 5-6 (7) flowered; peduncles ca. 5 mm long, lanate, sub-umbellate. Involucres campanulate (5) 6-9 mm high, (3.5) 4.5-5.2 mm wide; phyllaries arachnoid-ciliate, loosely appressed, purple; inner phyllaries elliptic-oblong, 6.5-8.2 mm long, 1.3-1.9 mm wide, tips acuminate; outer phyllaries lanceolate, 0.9-1.5 mm long, 0.7-0.9 mm wide. Pappus whitish; inner bristles 5.5-6.5 mm long, outer bristles 1-1.2 mm long. Corollas 8.8-10 mm long, reddish-purple, white glandular. Anthers 2.2-3.2 mm long. Achenes 2.7-3.6 mm long, pilose, 6-7 ribbed with 1 main rib on convex side. Chromosome number $n =$ ca. 17. Flowering and fruiting occur from Oct. to Dec.

This species is found in southwestern Jalisco as shown in Fig. 3. It grows in ravines of oak-pine forest and tropical deciduous forest at 650 to 800 m elevation in the Northern Uplands of the Sierra Madre del Sur. *Mexia* 1575 from San Sebastián, Jalisco appears to be a hybrid between *V. autumnalis* and *V. bealliae.*

REPRESENTATIVE SPECIMENS: México: Jalisco: Mountainsides above (north of) La Cuesta, *McVaugh* 20268 (ENCB, MICH); 5 km N El Tuito, Mpio. de Cabo Corrientes, *McVaugh* 25476 (MICH).

8. **Vernonia bealliae** McVaugh, Contr. Univ. Mich. Herb. 9: 479. 1972. TYPE: México: Jalisco: San Sebastián, *Nelson* 4098 (Holotype: GH. Isotype: US!).

Vernonia corymbiformus sensu Gleas. Bull. New York Bot. Gard. 4: 198. 1906, not *V. corymbiformis* DC.

Suffruticose, erect or sometimes arching, 1.5-3 m; stems almost glabrous to lightly floccose. Leaves cauline; leaf blades (7) 9-14 (16) cm long, (2) 3-7 (10) cm wide (length/width ratio ca. 2-3), widest at or slightly below the middle, lanceolate to lanceolate-ovate, glabrous to somewhat scabrous above, reticulate-veined, resinous, with glandular trichomes to almost glabrous below, apically acuminate to almost acute, basally cuneate, margins serrate; petioles (0.7) 1-2 (3.5) cm long, glabrate to pilose-hispid or almost tomentose. Inflorescences pyramidal, usually 1-3 dm wide. Heads 17-29 flowered; peduncles 1-3 cm long, strigose to resinous or glabrate, sub-umbellate in tight clusters. Involucres campanulate, (7.7) 9-11 (11.7) mm high, (5.5) 7-8 (8.3) mm wide; phyllaries glabrous, margins sometimes ciliate, loosely appressed, purple; inner phyllaries lanceolate, 6.3-9 mm long, 1-1.8 mm wide, tips awned, 0.2-1 mm long; outer phyllaries lanceolate, 2-5.6 mm long, 0.6-1.2 mm wide. Pappus white to straw colored; inner bristles 6-7 mm long, outer bristles 0.5-1.5 mm long. Corollas (8.5) 10-11.5 (12) mm long, reddish purple. Anthers (2.5) 3-4 mm long. Achenes ca. 4 mm long, densely white glandular when young, resinous when older. Flowering and fruiting occur from Feb. to May.

This species is distributed from Jalisco south to Michoacán as shown in Fig. 1. It grows in humid pine-oak-fir forests and barrancas on steep slopes and along streams, altitude 1620-2600 m, in the Northern Uplands of the Sierra de Parnaso, the Sierra de Perote, and Sierra de Coalcoman.

REPRESENTATIVE SPECIMENS: México: Jalisco: ca. 15 mi SE Autlán, *McVaugh* 10331 (DUKE, GH, MEX, MICH, NY, TEX); Michoacán: S. Torricillas, Coalcoman, *Hinton* 13674 (F, MO, NY, US).

9. **Vernonia barclayi** H. Robinson & C. F. Reed. Phytologia 27: 52. 1973. TYPE: México: Sonora: Sierra Tecuari;

slopes above Rancho El Banco along road between Alamos and Mil Pilas, Chihuahua, *A. S. Barclay & J. Arguellas* 2018. (Holotype: US! Isotype: REED).

Plants frutescent, ca. 2 m tall; stems striate, whitish tomentose. Leaf blades 4-10 cm long, 1.5-3.5 cm wide (length/width ratio ca. 3) widest below the middle, oblong-elliptic, downy above, tomentose below, apically acute, basally rounded, margins remotely and faintly toothed; petioles 2-3 mm long, whitish tomentose. Inflorescences subumbellate. Heads ca. 60 flowered; peduncles 1.5-2 cm long, whitish tomentose. Involucres campanulate, ca. 8 mm high, 10-12 mm wide; phyllaries arachnoid, tightly appressed in ca. 5 series, greenish with a slight tinge of purple; inner phyllaries lanceolate, ca. 6 mm long, ca. 1.5 mm wide, tips acuminate; outer phyllaries lanceolate, 2.5 mm long, 1 mm wide. Pappus whitish; inner bristles ca. 7 mm long, outer bristles 0.7 mm long. Corollas 12.5 mm long, reddish-purple. Anthers 3.5 mm long. Achenes 3.5 mm long, sparsely pilose-hispid, ca. 10 ribbed. Flowering and fruiting occur from April to May.

This species is known only from the type location in the state of Sonora along the road between Alamos, Sonora and Mil Pilas, Chihuahua (Fig. 5). It is locally abundant along moist ravines in the oak zone of Sierra Tecuari.

10. **Vernonia feddemae** McVaugh, Contr. Univ. Mich. Herb. 9(4): 480. 1972. TYPE: México: Tepic: ca. 5 km NE of Puga (ca. 15 km NE of Tepic), pastured lands among large boulders, with trees and shrubs, elev. ca. 1000 m, *Feddema* 846A (Holotype: MICH!).

Perennial herb, 1 m tall; stems striate, slightly pubescent. Leaves cauline, coriaceous; leaf blades 8-12 cm long, 3-5 cm wide (length/width ratio ca. 1.6-1.9), widest at the middle, elliptic, glabrate above, resinous-glandular and slightly downy below, apically acute, basally rounded-cuneate to slightly oblique, margins remotely toothed, revolute; petioles 2-5 mm long, downy. Inflorescences

pyramidal. Heads 3-5 flowered; peduncles ca. 1 cm long, pilose-hispid, multibracteate, almost subumbellate. Involucres cylindric, ca. 8 mm high, ca. 4 mm wide; phyllaries glandular-tomentose, loosely appressed, greenish-purple; inner phyllaries narrowly elliptic, ca. 4 mm long, ca. 1 mm wide, tips apiculate; outer phyllaries ovate, ca. 1.5 mm long, ca. 1 mm wide. Pappus whitish; inner bristles 4.5 mm long, outer bristles 0.9 mm long, scale-like. Corollas ca. 9 mm long, reddish-purple, white glandular. Anthers ca. 2.6 mm long. Achenes ca. 2.5 mm long, pilose, with ca. 9 or 10 ribs. Flowering and fruiting occur from August to September.

This species is known only from the type locality. This collection was made in pastured lands among large boulders, with trees and shrubs, at an elevation of ca. 1,000 m. As McVaugh (1972) noted, this species is related to others in the group by habit, but the repeated forking of the branches of the inflorescence and the long multibracteate peduncles are unique to this group and unique among Mexican Vernonias. All things considered, it is probably best placed among this group of Vernonias until other evidence suggests otherwise.

EXCLUDED SPECIES

Vernonia bolleana Sch. Bip. ex Seemann, Bot. Voy. Herald 297. 1856. TYPE: México: N. W. México, *Seeman s.n.* (Holotype: K! as photo MICH! Isotypes: P! G!). This species was placed by Gleason (1906) in subsection *Paniculatae* series *Verae* but it does not appear to belong here or in subsection *Paniculatae* series *Umbelliformes*. Most likely it should be placed in the genus *Bolanosa*.

LITERATURE CITED

GLEASON, H. A. 1906. A revision of the North American Vernonieae. Bull. N. Y. Bot. Gard. **4**: 144-243.

———. 1922. Vernonieae. North Amer. Fl. **33**: 52-95.

———. 1923. Evolution and geographical distribution of the genus *Vernonia* in North America. Amer. J. Bot. **10**: 187-202.

Jones, S. B. 1974. Vernonieae (Compositae) chromosome numbers. Bull. Torrey Bot. Club. **101**: 31-34.

Mabry, T. J., Z. Abdel-Baset, W. G. Padolina, & S. B. Jones. 1975. Systematic implications of flavonoids and sesquiterpene lactones in species of *Vernonia*. Biochem. System. & Ecology. **2**: 185-192.

Willis, J. C. 1966. A dictionary of the flowering plants and ferns. 7th ed. Revised by H. K. A. Shaw. 1214 & LIII pp.

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THE VASCULAR FLORA OF THE GROS MORNE NATIONAL PARK COASTAL PLAIN, IN NEWFOUNDLAND

André Bouchard and Stuart Hay

During the summer of 1972 field studies were carried on in the coastal plain of the Gros Morne National Park of Newfoundland in order to provide baseline information on its vegetation. These data were then used, in conjunction with air photos, to produce a vegetation map and a vegetation analysis of the area (Bouchard, 1974). The field studies produced an abundance of data not apparent or easily extracted from the more generalized vegetational analysis. This fact, together with the fact that few floristic studies specific to the maritime provinces have been written, led to the preparation of this flora of the coastal plain of the Gros Morne National Park.

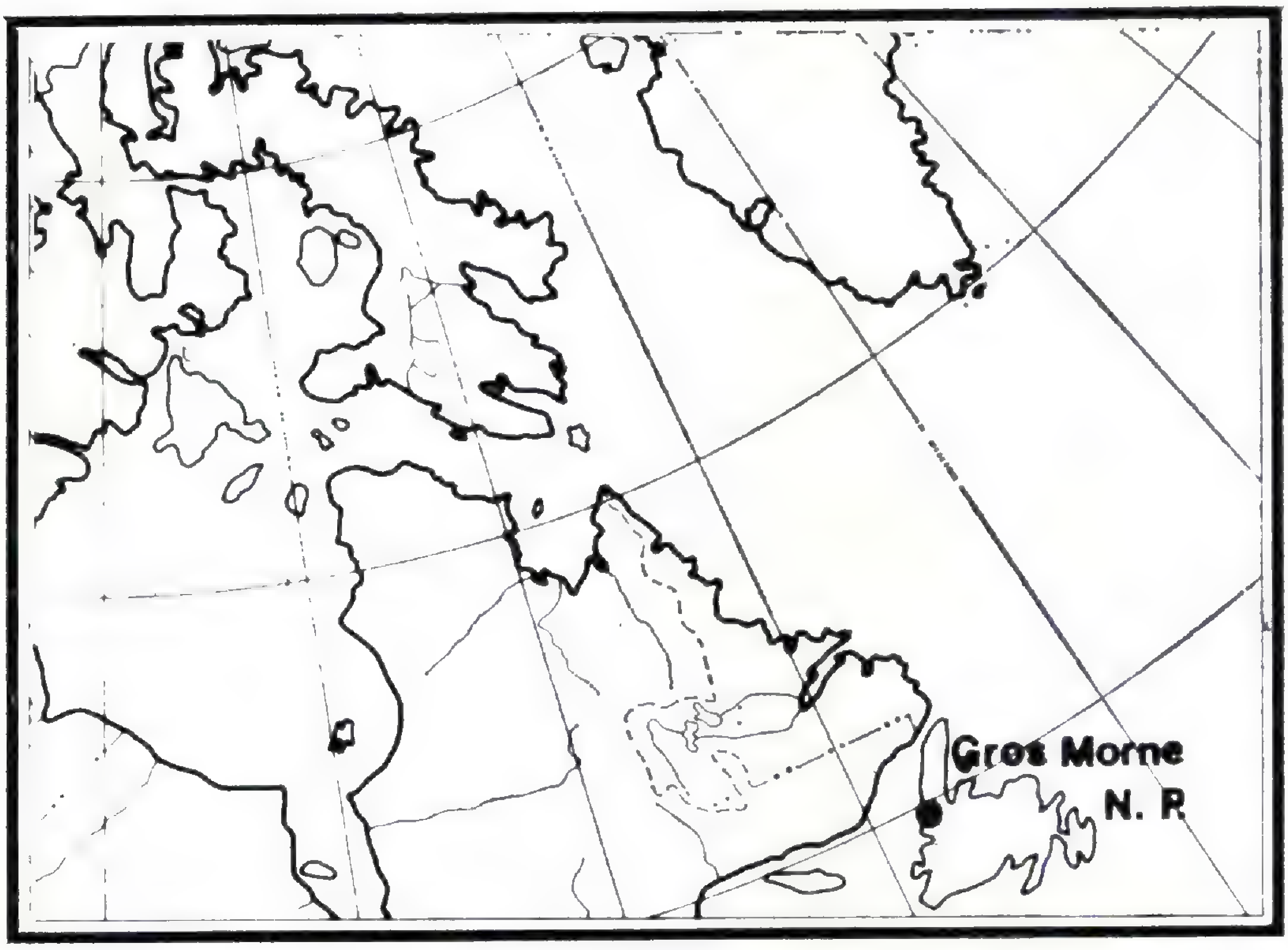

Figure 1. Gros Morne National Park on the Island of Newfoundland, in Eastern Canada.

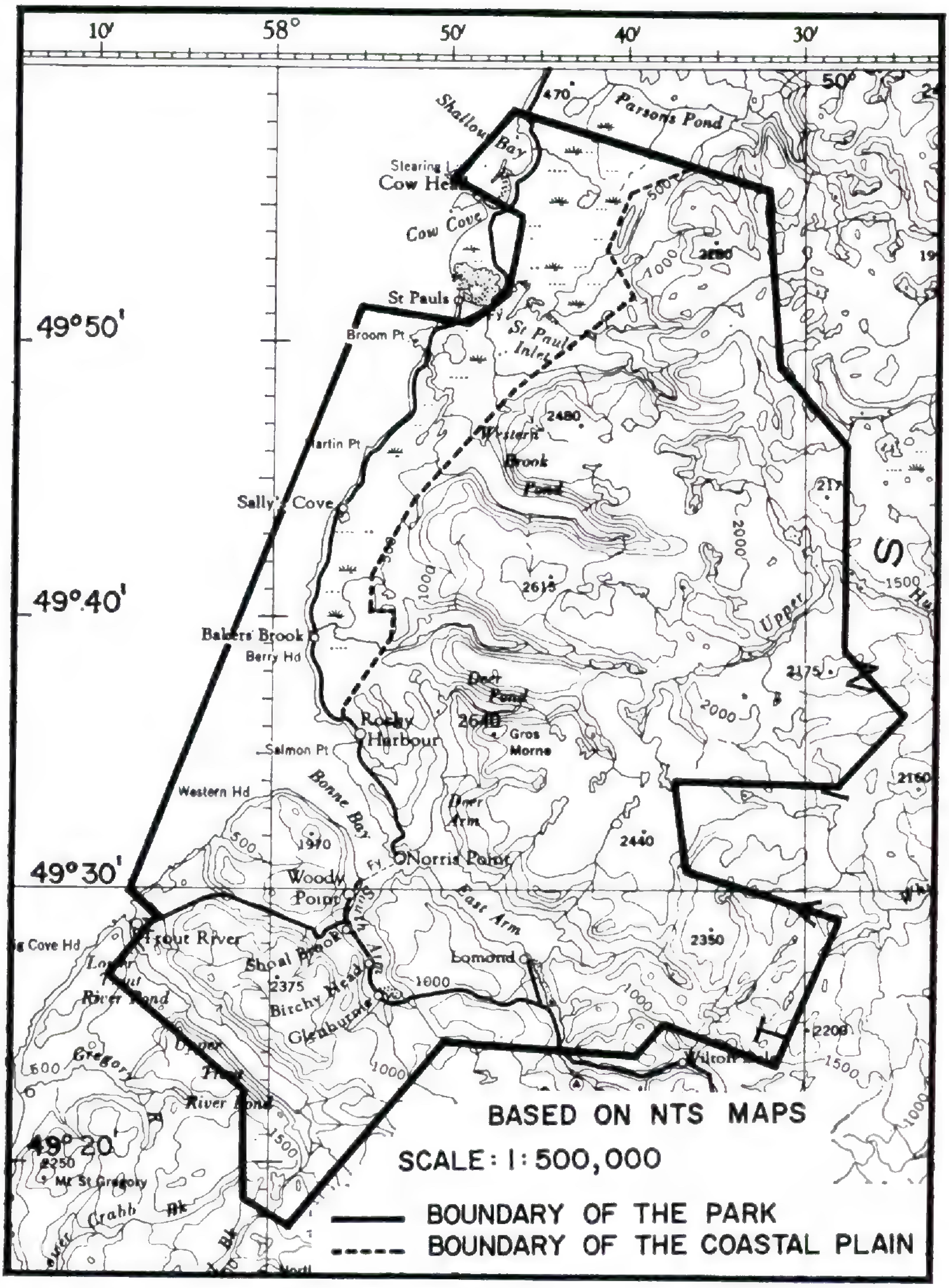

Figure 2. Gros Morne National Park.

DESCRIPTION OF THE AREA

Geography and Physiography

Gros Morne National Park is situated on the western coast of Newfoundland (Figs. 1 and 2). The coastal plain area of the park extends from Rocky Harbour in the south to Lower Head in the north, a straight line distance of 44 kilometers (27 miles) or a coastline distance of 55 kilometers (34 miles).

The shoreline is composed primarily of low cliffs of loose and unconsolidated glacial and marine material alternating here and there with rocky points or headlands and occasional dune formations. Back from the shoreline is a gently rolling plain of up to 150 meters elevation. This plain extends inland distances of from four to thirteen kilometers (two and one half to eight miles) to the base of the high altitude Long Range Mountains, the dominant physiographic feature of the region. These mountains, ranging to 806 meters (2644 feet), have four "fjords" opening on the coastal plain. Western Brook Pond, a "fresh water fjord", is the most spectacular and is easily seen from the study area.

Geology

The coastal lowland is composed mainly of three groups of interbedded sedimentary formations, the Humber Arm Group, the Green Point-St. Pauls Group and the St. George Group which alternate in bands parallel to the coast (Geologic map: Baird, 1958). Except for some breccias of middle Cambrian and some Pennsylvanian and/or Mississippian sedimentaries, all three groups are Ordovician.

The Humber Arm Group is found throughout the coastal plain. It is composed mainly of greyish green and grey sandstones, conglomerates, and grey shales (Baird, 1958). In the northern section of the plain, the Green Point-St. Pauls Group (composed of thin bedded limestone, abundant Cow Head type breccias, shale and siltstone), alternates with the Humber Arm Group. In the southern section, the

St. George Group, composed of massive grey, blue-grey, and white limestone dolomite, buff weathered, white dolomite and interbedded shales, constitutes an important part of the bedrock. The breccias are most abundant at Broom Point and Cow Head. The sedimentary rocks of the coastal lowland are thickly buried beneath marine and glacial deposits, except for a few rock ridges and headlands. This complex array of glacial and marine features is easier to understand when interpreted in terms of a piedmont glacier phase characterized by expanded-foot valley glaciers formerly terminated in a sea that once stood about 100 meters higher and transgressed inland to that elevation as the glaciers receded up the troughs of the Long Range Mountains (Grant, 1970 and 1973).

Climate

The climate of Newfoundland is best known from the work of Hare (1952) and this sketch is drawn primarily from his data. Three climatic factors related to the geographical position of Newfoundland appear to be of overwhelming dominance in determining the vegetation of the coastal plain area. These are the moderating influence of the ocean, the strong and prevailing winds coming from the Gulf of St. Lawrence, and a continual moisture excess.

A cool climate with a short growing season is responsible for the boreal aspect of the vegetation. The mean air temperature (mean of daily maximum and minimum) in July is between 12.8°C (55°F) and 15.6°C (60°F). In January, it is between −9.4°C (15°F) and −6.7°C (20°F). The temperature of the sea surface, in mid July, for the study area is between 10°C (50°F) and 12.8°C (55°F). The vegetative growing season ranges from 140 to 150 days. The start of the vegetative season (mean air temperature higher than 6.1°C (43°F)) is between May 20 and May 30. For comparison, it is approximately April 10 for Montreal and Ottawa.

Relatively high precipitation, low potential evapotranspiration and poor water drainage due to the general flat-

ness of this lowland have resulted in the formation of large raised bogs. The mean annual precipitation is between 102 and 114 cm. The potential evapotranspiration, or the "landscape water need", is between 43 and 48 cm, leaving an annual moisture surplus greater than 55 cm. The mean annual snow fall ranges from 317.5 to 380 cm.

The predominant southwest on-shore winds are an important environmental factor responsible for the structure of several plant communities, especially the fir and white spruce scrub of the seashore and the black spruce and dwarf laurel dwarf scrub.

Vegetation

Although the coastal plain appears to be quite simple from a physiographic point of view, the vegetation is relatively complex.

The extensive flat wet terrains characteristic of the coastal plain are mostly covered with large raised bogs. Sedge meadows (or fens) and american larch scrub colonize the richer wet sites of this nearly level ground.

The black spruce scrub is the dominant woody community of the wet oligotrophic sites of this lowland. The mesic and more protected areas support forests of balsam fir.

Black spruce and dwarf laurel dwarf scrub are usually on the wind exposed moraines. These are found more frequently toward the Long Range Mountains where wind exposed habitats prevail. In a few cases, the extremely exposed sections are more or less barren and colonized by alpine bearberry, diapensia and alpine azalea, otherwise found on the top of the Long Range Mountains.

A web of meandering freshwater creeks is found throughout the lowland and often dissects the raised bogs. Alder swales are common on those sites. Around the larger lakes, aquatic communities are found but are usually not very rich in species. However, interesting elements such as water lobelia and creeping spearwort can be seen.

Small tidal flats, within the park boundaries, are located on the north shore of St. Pauls Inlet. Halophytic plant

communities, ranging from large monospecific populations of samphire to closed herbaceous communities of salt marsh sedge, colonize the flats.

Several plant communities are restricted to the narrow band of land between the shoreline and the road (Figure 2). The common scrub community is a wind shaped krummholz of balsam fir and white spruce. A mosaic of herbaceous plant communities exists between the barren, gravelly beaches and the krummholz, or between the beach and the road where the krummholz has been logged. Beachgrass colonizes the dunes formed at the mouth of Stanford River (Shallow Bay) and at the mouth of Western Brook. The few rocky cliffs along the seashore have a very sparse vegetation.

The seashore has received most of the human impact. The narrow band of land, between the shoreline and the road, has been used for settlements. The small villages of Downes Point south of Shallow Bay, Sally's Cove and Green Point, are situated on the seashore. The remainder of this thin band of land is sporadically occupied by fishermen during spring and summer. Although small potato gardens and hay fields are found here and there, the impact of cultivation on the coastal plain is limited. On the other hand, sheep, horses, and cows, left to range freely along the coast and the road, have had considerable impact on the nature of the shoreline's plant communities. The road and the settlements have also permitted the introduction of numerous weed species.

Logging and fire are two other sources of disturbance on the coastal plain. Because of the general wetness of this lowland, the fire produced communities are very restricted in size. Fire is responsible for the white birch scrub and the dwarf scrub of dwarf laurel and low sweet blueberry. The fir forests have been intensively logged and therefore replaced by successional communities. These are either dense homogenous second growth of balsam fir or heterogenous second growth of balsam fir with deciduous shrubs.

PREVIOUS FLORISTIC STUDIES

The western coast of Newfoundland has attracted several botanists. Bachelot de la Pylaie, a French naturalist, made two trips to Newfoundland (Leroy, 1957), the first one in 1816 and the second one in 1819-20. He actually spent fifteen days at St. George's Bay and eight days at Ingornachoix. This first locality is south and the latter is north of the Gros Morne National Park. Unfortunately the vascular plant section of his flora was not published. His important herbarium collections are kept at the National History Museum of Paris.

At the end of the last century, Reverend Arthur C. Waghorne did some collecting in regions south and east of the park area. His findings and studies of other botanists were published in the form of a flora (Waghorne, 1893, 1895, 1898). Most of the material was named by Professor Macoun of Ottawa. His flora is an enumeration by taxonomic order. Localities and phenology data are given for numerous species.

In the first part of this century Professor Fernald of Harvard University directed a series of botanical trips in western Newfoundland (Fernald, 1911, 1926-27, 1933). His studies of this area were done mainly around Bonne Bay, just south of the Coastal Plain. Cow Head (within the Coastal Lowland) was visited by Wiegand in 1910 (Fernald, 1911). Plants such as *Botrychium lunaria, Arabis alpina,* and *Gentiana nesophila* were found, among others, on the interesting brecchia formation. On the wet conglomerate limestone and calcareous sandstone cliffs and ledges was found the type specimen of *Cochlearia cyclocarpa* (Blake, 1914).

After visiting numerous localities, Fernald (1911, 1918) wrote that the boreal and even the arctic floras are abundantly represented with some elements of the southern coastal types. This coastal element in Newfoundland's flora is fascinating and deserves special attention.

These coastal plants are divided in two subclasses by Fernald. These are: (1) the Canadian or Alleghenian plants common to Newfoundland, Nova Scotia, New Brunswick, and coastwise New England, but unknown in easternmost Quebec and Labrador, and (2) Carolinian plants common to Newfoundland, Nova Scotia, Cape Cod and adjacent islands, Long Island or coastal and southern New Jersey, but rare or unknown inland or in continental eastern Canada. *Schizaea pusilla* is an example of this second grouping.

Fernald (1911), after considering other possibilities, made the interesting hypothesis that these coastal plants would have crossed to Newfoundland by a strip of sands and similar soils stretching, with only slight interruptions, from the south Atlantic coast to Newfoundland. This land bridge of siliceous soils would have been attractive to species such as *Pinus resinosa, Schizaea pusilla* and *Hudsonia ericoides* of highly siliceous regions pushing successfully across the bridge to Newfoundland (Fernald, 1911). On the other hand this land bridge would have been unattractive to species such as *Thuja occidentalis* and *Viburnum alnifolium.*

The Long Range Mountains of the Western Coast constitute the eastern boundary of the study area. Some plants of this western section of Newfoundland (Fernald, 1918) are species of high arctic-alpine range. In America, these species are abundant mainly in the arctic archipelago or in the Canadian Rocky Mountains. Plants of these Long Range Mountains and of other areas in the Gulf of St. Lawrence, especially endemics, were the basis for the famous nunatak theory of Fernald (1925). The ideas were discussed in "Persistence of plants in unglaciated areas of boreal America" (Fernald, 1925).

Recently Damman (1965) has shown that most of the species distributions can be satisfactorily explained by present climatic and edaphic conditions.

Much field work and more publications are still needed on Newfoundland's flora. The only complete checklist of

the vascular plants was published 20 years ago (Rouleau, 1956).

METHODS

Selection of Stands

The two basic objectives in stand selection were to cover the range of vegetation composition and the geographical extent of the coastal plain. Homogeneity of the components over an area of 2 to 4 hectares on a uniform topographical unit or a series of uniform units was the criterion for stand selection. The stands were selected along the ground truth survey transects for air photo correlation. For certain rare types, such as creekbeds, specifically because of size restrictions, this criterion could not be universally applied.

Natural communities were quantitatively sampled where grazing by sheep, cows and horses, in addition to logging and other human high intensity activities, were not obvious. Preferential sampling of natural undisturbed communities and/or communities where the presence of man has been erased by an even maturing second growth vegetation is due to the emphasis on wilderness in National Park planning and the limited time available.

Disturbed areas were visited, the vegetation was described and the flora inventoried, but no extensive studies were done. Specimen collections were also done in numerous areas that were not systematically sampled, as field work was progressing.

Collection of Field Data

In the nonforested communities, the frequency was assessed by use of 20 square meter quadrats randomly spaced following the methodology used by Curtis (1959).

In the forest communities, the Quarter Method (Cottam and Curtis, 1956, Curtis, 1959, and further elaborated by Maycock, 1963) was used to measure the composition of the arboreal and sapling stratum in each stand. Usually 30 random points were recorded, although in restricted types of vegetation fewer were taken. All individuals with

a d.b.h. (diameter at breast height) greater than 10.2 centimeters (four inches) were considered as trees, between 2.5 cm (one inch) and 10.2 cm (four inches) as saplings and those with a d.b.h. less than 2.5 cm (one inch) as seedlings. In the case of several species (*Alnus rugosa, Pyrus decora,* etc.) the normal size criteria were not easily applied because they may be present as understory shrubs or never attain the canopy. Thus in these circumstances saplings of these species were recorded only when tree-sized individuals were also present. At all other sampling points a meter square quadrat was placed, and all herb, shrub, and tree seedling species present were recorded. In all of these communities a full presence list of the vascular plants was made.

Treatment of Stand Data

In each stand, a frequency value was determined for each tree species by calculating the percentage of points at which it was present.

Stand frequency values for herbs, shrubs and seedlings were obtained by determining percentage occurrence in quadrats of a meter square.

A commonness index was computed for every species within each vegetation type that was quantitatively studied. The commonness index may range from 0 to 10,000 for a species within a community type and is obtained by multiplying the average frequency-of-occurrence in sample points or quadrats within a community type by the percent of stands within a community type in which the species was present (Ohmann and Ream, 1971).

This commonness index was used to evaluate the importance of the majority of the species mentioned in the present study.

A species is considered to be "very common" with a commonness index ranging from 5,000 to 10,000, "common" with values ranging from 1,000 to 4,999, and "uncommon" with values of less than 1,000. Many uncommon species can easily be found within the designated vegeta-

tion types; however, the probability of finding such a species is less than 10% in a randomly selected meter quadrat or point. Locating rare species normally requires extensive field work. Of course such species are the ones whose status will change as more knowledge is accumulated on the flora of the coastal plain.

Each species was evaluated for its occurrence in the following vegetation types or mapping units used for the vegetation maps and for the vegetation analysis (Bouchard, 1974).

A Second growth forest of balsam fir (*Abies balsamea*). Most of the canopy is 8 meters or more above the ground. The associated tree species are usually white spruce (*Picea glauca*) and white birch (*Betula papyrifera*). Less often black spruce (*Picea mariana*) constitutes an important element of the balsam fir stands.

B1 Black spruce scrub. Black spruce, 1 to 4 m. tall, is the dominant shrub over a peat moss (*Sphagnum*) mat. Balsam fir is always an important member of this community. Speckled alder (*Alnus rugosa*) becomes increasingly important in wetter habitats. Within this unit some black spruce stands may reach 8 m. in height.

B2 American larch (*Larix laricina*) scrub. This homogenous open scrub, 1 to 3 m. tall, is characterized by a rich ground flora commonly composed of elements such as tall meadow rue (*Thalictrum polygamum*), low birch (*Betula pumila*) and sedges.

B3 Wind shaped balsam fir and white spruce scrub. These krummholz of balsam fir are found along the seashore. White spruce is usually present and dominates some small sections. The flattened crowns vary in height from less than 1 m., near the sea, to about 6 m., inland. Mature stands are composed of a few large trees with typically flattened crowns but nearly pure stands of saplings also occur. The understory of this scrub has been heavily grazed by sheep and horses.

B4 Homogenous second growth scrub of balsam fir. The height of this dense scrub varies from 1 to 6 m.

B5 Heterogenous second growth scrub of balsam fir and deciduous shrubs. Several deciduous shrubs such as mountain maple (*Acer spicatum*), white birch, raspberry (*Rubus idaeus*), green alder (*Alnus crispa*) and speckled alder, with heights varying from 1 to 6 m., are common in this balsam fir scrub. Usually there are scattered large trees of white birch, balsam fir and white spruce. Open forests of white birch with lower strata of balsam fir are included in this mapping unit.

B6 White spruce scrub. Balsam fir is the co-dominant of this 4 to 8 m. tall scrub. This rare type of vegetation is restricted in size on the coastal plain and heavily disturbed by man's activities.

B7 White birch scrub. The height of this heterogenous community varies from 2 to 6 m. The understory is composed of diverse shrubs and herbs.

B8 Tall meadow rue, sweet gale (*Myrica gale*), meadow sweet (*Spiraea latifolia*) and speckled alder scrub. These shrubs, 1 to 2 m. tall, colonize the flood plains found along meandering fresh water creeks and rivers. Along the larger creeks and rivers, speckled alder is the dominant shrub with scattered trees of larch, white birch, white spruce and black spruce. The ground flora is abundant and diversified.

C1 Black spruce and dwarf laurel (*Kalmia angustifolia*) dwarf scrub. This community, of less than 50 cm. in height, varies from pure formations of black spruce to more or less heterogenous formations of black spruce in which ericaceous shrubs, especially dwarf laurel, are co-dominants.

C2 Ericaceous dwarf scrub. Dwarf laurel, low sweet blueberry (*Vaccinium angustifolium*), Labrador tea (*Ledum groenlandicum*) and rhodora (*Rhododendron*

canadense) are the dominants. These average 25 cm. in height.

D Peat moss and reindeer moss (*Cladina*) bog. Numerous ponds or "flashets" are present. Tufted club rush (*Scirpus cespitosus*) is the dominant vascular plant. Baked apple (*Rubus chamaemorus*) and black crowberry (*Empetrum nigrum*) are very common. The ericaceous shrubs, leather leaf (*Chamaedaphne calyculata*), dwarf laurel, Labrador tea, bog laurel (*Kalmia polifolia*), bog rosemary (*Andromeda glaucophylla*) and small cranberry (*Vaccinium oxycoccos*), occur very frequently, are all confined to a lower stratum and are usually less than 5 cm. in height.

E Sedge meadow. Communities of *Carex* found in wet areas. One or several sedges such as starved sedge (*Carex exilis*), villose sedge (*Carex lasiocarpa*) and livid sedge (*Carex livida*) dominate this vegetation type. These communities are also often invaded by shrubs such as sweet gale, low birch and larch. Hydric herbaceous plants such as buckbean (*Menyanthes trifoliata*) and water horsetail (*Equisetum fluviatile*) are frequent.

F Mosaic of herbaceous plant communities. Found along the seashore and the inlets, these communities form a thin band of vegetation when adjacent to barren gravelly or sandy beaches. Red fescue grass (*Festuca rubra*), junegrass (*Poa pratensis*), redtop (*Agrostis alba*) and numerous introduced species are the most common plants. Indigenous plants such as beachhead iris (*Iris hookeri*), three-toothed cinquefoil (*Potentilla tridentata*) and bird's eye primrose (*Primula laurentiana*) have persisted in these communities that are heavily grazed by sheep, horses and cows.

G Dunes and sandy seashore community. Extensive areas are colonized by beachgrass (*Ammophila breviligulata*) and also heavily grazed by sheep, horses and cows.

H Rocky cliffs community. This very sparse herbaceous vegetation is composed commonly of seaside plantain (*Plantago juncoides*). Roseroot (*Sedum rosea*) is also a common plant.

I Tidal flat communities. These halophytic plant communities range from large monospecific populations of samphire (*Salicornia europaea*) on bare ground to closed herbaceous communities of salt marsh sedge (*Carex salina*).

J Cleared areas. These have been drastically changed by human activities (settlements, gardens, gravel pits, etc.). The vegetation is mainly composed of introduced plants.

The nomenclature, except for a few species, follows Gray's Manual of Botany (Fernald, 1950). The taxonomical arrangement of families follows Rouleau (1970).

The specimens have been deposited in the Gros Morne National Park Herbarium, in the National Herbarium of Canada (CAN) and in the Marie-Victorin Herbarium of University of Montreal (MT).

THE VASCULAR FLORA

Lycopodiaceae

Lycopodium annotinum: Rare in the ericaceous dwarf scrub.

Lycopodium complanatum: Rare in the ericaceous dwarf scrub.

Lycopodium lucidulum: Rare in the second growth forests of balsam fir, in the white birch scrub, in the creek bed communities and in the black spruce and dwarf laurel dwarf scrub.

Lycopodium obscurum: Rare in the second growth forests of balsam fir.

Selaginellaceae

Selaginella selaginoides: Uncommon in the american larch scrub, in the peatmoss and reindeer moss bogs and in the sedge meadows.

Isoetaceae

Isoetes muricata: Uncommon in the aquatic communities.

Equisetaceae

Equisetum arvense: Common in the black spruce scrub, in the white birch scrub and cleared areas; uncommon in the second growth forests of balsam fir, in the american larch scrub, in the creek bed communities, in the black spruce and dwarf laurel dwarf scrub, in mosaic of herbaceous plant communities, in the dunes and sandy seashore communities and in the rocky cliff communities.

Equisetum fluviatile: Very common in the american larch scrub; common in the sedge meadows and in the aquatic communities; uncommon in the black spruce scrub and in the peatmoss and reindeer moss bogs.

Equisetum palustre: More or less common in the american larch scrub; uncommon in the black spruce scrub, in the creek bed communities, and in the sedge meadows; also found in some ponds of peatmoss and reindeer moss bogs.

Equisetum sylvaticum: More or less common in the black spruce scrub; uncommon in the second growth forests of balsam fir and in the white birch scrub.

Equisetum variegatum: Uncommon in the american larch scrub.

Ophioglossaceae

Botrychium lunaria: Very rare in the mosaic of herbaceous plant communities along the seashore. Found at Lower Head.

Botrychium matricariaefolium: Rare, found on a grazed hillside at Broom Point.

Botrychium multifidum: Uncommon in the creek bed communities and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Botrychium virginianum: Uncommon in the american larch scrub.

Osmundaceae

Osmunda cinnamomea: Uncommon in the black spruce scrub, in the american larch scrub and in the creek bed communities.

Osmunda regalis: Very rare. Found on the north shore of Round Steady on the edge of an heterogenous second growth scrub of balsam fir and deciduous shrubs.

Athyriaceae

Athyrium filix-femina: Uncommon in the second growth forests of balsam fir, in the black spruce scrub, in the white birch scrub, in the creek bed communities, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the cleared areas.

Cystopteris fragilis: Uncommon and restricted to the rocky cliff communities.

Aspidiaceae

Onoclea sensibilis: More or less common in creek bed communities; uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets.

Pteretis pensylvanica: Uncommon in the creek bed communities.

Dryopteridaceae

Dryopteris cristata: Uncommon in the american larch scrub and in the creek bed communities.

Dryopteris disjuncta: Common in black spruce scrub; uncommon in the heterogenous second growth scrub of balsam fir and deciduous shrubs, in the white birch scrub, and in the creek bed communities; rare in the second growth forests of balsam fir.

Dryopteris filix-mas: Uncommon to rare, found on a logging trail, just north of Berry Hill.

Dryopteris phegopteris: Rare in the second growth forests of balsam fir, in the black spruce scrub, in the heterogenous second growth scrub of balsam fir and deciduous shrubs and in the creek bed communities.

Dryopteris spinulosa: Very common in the second growth forests of balsam fir, common in the heterogenous second growth scrub of balsam fir and deciduous shrubs, uncommon in the black spruce scrub, in the wind shaped balsam fir and white spruce scrub, in the homogenous second growth scrub of balsam fir, in the white birch scrub and in the creek bed communities.

Dryopteris thelypteris: Uncommon in the creek bed communities.

Dryopteris × bootii: Rare to uncommon, found on a logging trail in a black spruce scrub, at Sally Cove.

Polystichum braunii: Rare in creek bed communities.

Polypodiaceae

Polypodium virginianum: Rare, found on a large boulder near Western Brook Pond outlet.

Pinaceae

Abies balsamea: Very common in the second growth forests of balsam fir, in the black spruce scrub, in the wind shaped balsam fir and white spruce scrub and in the homogenous second growth scrub of balsam fir; very common to common in the heterogenous second growth scrub of balsam fir and deciduous shrubs, uncommon in the american larch scrub, in the white birch scrub, in the creek bed communities, in the black spruce and dwarf laurel dwarf scrub, in the peatmoss and reindeer moss bogs, in the sedge meadows, in the rocky cliff communities, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the barrens communities; rare in ericaceous dwarf scrub.

Larix laricina: Very common in the american larch scrub; common in the sedge meadows; uncommon in the black spruce scrub, in the white birch scrub, in the creek bed communities, in the black spruce and dwarf laurel dwarf scrub, in the peatmoss and reindeer moss bogs, and in the barrens communities.

Picea glauca: Very common in the white spruce scrub; common in the wind shaped balsam fir and white spruce scrub; more or less common in second growth forests of balsam fir; uncommon in the homogenous second growth scrub of balsam fir; uncommon in the heterogenous second growth scrub of balsam fir and deciduous shrubs, in the white birch scrub, in the creek bed communities, in the rocky cliff communities, and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Picea mariana: Very common in the black spruce scrub and in the black spruce and dwarf laurel dwarf scrub; uncommon but locally abundant in the second growth forests of balsam fir; uncommon in the american larch scrub, in the creek bed communities, in the peatmoss and reindeer moss bogs, in the sedge meadows, and in the barrens communities; rare in the ericaceous dwarf scrub.

Cupressaceae

Juniperus communis: Common in the barrens communities; uncommon in the american larch scrub, in the homogenous second growth scrub of balsam fir, in the black spruce and dwarf laurel dwarf scrub, in the ericaceous dwarf scrub, in the peatmoss and reindeer moss bogs, in the sedge meadows, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the rocky cliff communities.

Juniperus horizontalis: Uncommon in the american larch scrub, in the black spruce and dwarf laurel dwarf scrub and in the rocky cliff communities.

Taxaceae

Taxus canadensis: Common in the second growth forests of balsam fir and in the heterogenous second growth scrub of balsam fir and deciduous shrubs; more or less common in black spruce scrub; uncommon in the white birch scrub and in the creek bed communities.

Nymphaeaceae

Nuphar variegatum: Uncommon but locally abundant in aquatic communities.

Ranunculaceae

Aconitum bicolor: A rare introduced plant for the coastal plain, found along a small stream at Shallow Bay.

Actaea rubra: Uncommon in the creek bed communities.

Anemone canadensis: Very rare. Found on a gravelly outwash, along Stag River.

Caltha palustris: Common in the american larch scrub and in the creek bed communities; uncommon in the black spruce scrub and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Coptis groenlandica: Common in the black spruce scrub; uncommon in the second growth forests of balsam fir, in the black spruce and dwarf laurel dwarf scrub, in the ericaceous dwarf scrub, in the peatmoss and reindeer moss bogs and in the sedge meadows.

Ranunculus abortivus: Uncommon in the creek bed communities.

Ranunculus acris: Common in the cleared areas; uncommon in the creek bed communities, in the rocky cliff communities and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Ranunculus cymbalaria: Uncommon and restricted to rocky cliff communities.

Ranunculus pensylvanicus: Very rare. Found on a gravelly outwash, along Stag River.

Ranunculus repens: Uncommon in the wind shaped balsam fir and white spruce scrub, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the cleared areas.

Ranunculus reptans: Rare in the aquatic communities.

Thalictrum alpinum: Common in the american larch scrub.

Thalictrum polygamum: Very common in the american larch scrub and in the creek bed communities; uncommon in the black spruce scrub, in the sedge meadows, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the tidal flat communities.

Sarraceniaceae

Sarracenia purpurea: Very common in the sedge meadows; common in the american larch scrub and in the peatmoss and reindeer moss bogs; uncommon in the black spruce and dwarf laurel dwarf scrub; rare in the ericaceous dwarf scrub.

Urticaceae

Urtica gracilis: Rare in the creek bed communities.

Betulaceae

Alnus crispa: Common in the heterogenous second growth scrub of balsam fir and deciduous shrubs and in the white birch scrub; uncommon in the second growth forests of balsam fir, in the black spruce scrub, in the creek bed communities, in the cleared areas and in the barrens communities.

Alnus rugosa: Very common in the creek bed communities; common in the black spruce scrub and in the heterogenous second growth scrub of balsam fir and deciduous shrubs, uncommon in the second growth forests of balsam fir, in the american larch scrub, in the black spruce and dwarf laurel dwarf scrub, in the sedge meadows and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Betula borealis: Rare in the black spruce and dwarf laurel dwarf scrub.

Betula michauxii: Common in the sedge meadows and around the small ponds of the peatmoss and reindeer moss bogs.

Betula papyrifera: Very common in the white birch scrub; common in the second growth forests of balsam fir and in the heterogenous second growth scrub of balsam fir and deciduous shrubs; uncommon in the black spruce scrub, in the wind shaped balsam fir and white spruce scrub, in the homogenous second growth scrub of balsam fir, in the creek bed communities, in the sedge meadows and in the barrens communities; rare in the peatmoss and reindeer moss bogs, in the black spruce and dwarf laurel dwarf scrub and in the ericaceous dwarf scrub.

Betula pumila: Very common in the american larch scrub; common in the black spruce scrub; uncommon in the creek bod communities, in the black spruce and dwarf laurel dwarf scrub and in the peatmoss and reindeer moss bogs; rare in the ericaceous dwarf scrub.

Corylaceae

Corylus cornuta: Uncommon in the heterogenous second growth scrub of balsam fir and deciduous shrubs; rare in the creek bed communities.

Myricaceae

Myrica gale: Very common in the american larch scrub and in the sedge meadows; common in the creek bed communities, in the black spruce and dwarf laurel dwarf scrub, in the ericaceous dwarf scrub and in the peatmoss and reindeer moss bogs; uncommon in the black spruce scrub, mosaic of herbaceous plant communities along the seashore and the inlets and in the tidal flat communities.

Portulacaceae

Montia lamprosperma: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets.

Caryophyllaceae

Arenaria lateriflora: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets.

Arenaria rubella: Rare. Found in a rocky cliff community, along the shoreline of the forebay of Western Brook Pond.

Arenaria peploides: Uncommon in the rocky cliff communities.

Cerastium arvense: Rare. Found in a rocky cliff community, along the shoreline of the forebay of Western Brook Pond.

Cerastium vulgatum: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets, in the rocky cliff communities and in the cleared areas.

Sagina nodosa: Uncommon in the rocky cliff communities.

Sagina procumbens: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets.

Spergularia canadensis: Uncommon in the tidal flat communities.

Stellaria longipes: Uncommon but locally abundant in the cleared areas.

Stellaria media: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets and in the rocky cliff communities.

Chenopodiaceae

Atriplex patula: Uncommon in the rocky cliff communities.

Chenopodium album: Found along the road, at St. Pauls.

Salicornia europaea: Common in the tidal flat communities.

Salsola kali: Uncommon in the sandy seashores.

Polygonaceae

Polygonum aviculare: Found along the road, at St. Pauls.

Polygonum fowleri: Rare in the mosaic of herbaceous plant communities along the seashore and the inlets. Found at St. Pauls.

Polygonum persicaria: Found along the road, at St. Pauls.

Polygonum viviparum: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets and in the rocky cliff communities.

Rumex acetosa: Uncommon to rare in the mosaic of herbaceous plant communities along the seashore and the inlets.

Rumex acetosella: Uncommon to rare in the mosaic of herbaceous plant communities along the seashore and the inlets and in the cleared areas.

Rumex mexicanus: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets.

Rumex orbiculatus: Uncommon in the american larch scrub, rocky cliff communities and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Hypericaceae

Hypericum virginicum: Uncommon in the sedge meadows, in the tidal flat communities and in the aquatic communities.

Violaceae

Viola cucullata: Common in the creek bed communities; uncommon in the american larch scrub and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Viola incognita: Uncommon in the american larch scrub, in the heterogenous second growth scrub of balsam fir and deciduous shrubs, in the white birch scrub, in the creek bed communities, in the rocky cliff communities and in the mosaic of herbaceous plant communities along the seashore and the inlets; rare in the second growth forests of balsam fir and in the wind shaped balsam fir and white spruce scrub.

Viola labradorica: Rare in the sedge meadows.

Viola nephrophylla: Rare in the creek bed communities.

Viola pallens: Uncommon in the american larch scrub, in the creek bed communities and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Viola renifolia: Uncommon in the second growth forests of balsam fir, in the black spruce scrub, in the heterogenous second growth scrub of balsam fir and deciduous shrubs, in the white birch scrub, in the creek bed communities and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Viola renifolia × *pallens:* Rare in the heterogenous second growth scrub of balsam fir and deciduous shrubs.

Viola septentrionalis: Rare in the creek bed communities.

Brassicaceae

Cakile edentula: Uncommon in the rocky cliff communities and on the sandy seashores.

Capsella bursa-pastoris: Uncommon in the rocky cliff communities and in the cleared areas.

Cardamine pensylvanica: Found on a gravelly outwash along Stag River.

Cochlearia cyclocarpa: Uncommon in the rocky cliff communities.

Draba glabella: Rare. Found in a rocky cliff community, along the shoreline of the forebay of Western Brook Pond.

Draba incana: Uncommon in the rocky cliff communities.

Salicaceae

Salix candida: Uncommon in the american larch scrub, in the creek bed communities and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Salix discolor: Uncommon in the black spruce scrub, in the american larch scrub, in the white birch scrub and in the creek bed communities.

Salix lucida: Found on the western shore of Western Brook Pond.

Salix pellita: Uncommon in the american larch scrub.

Salix planifolia: Rare. Found on a gravelly outwash, along Stag River.

Salix serissima: Rare in the american larch scrub.

Populaceae

Populus balsamifera: A few individuals in a white birch scrub, on the southwest side of Western Brook Pond.

Ericaceae

Andromeda glaucophylla: Very common in the peatmoss and reindeer moss bogs and in the sedge meadows; common in the american larch scrub; uncommon in the black spruce and dwarf laurel dwarf scrub and in the ericaceous dwarf scrub.

Arctostaphylos alpina: Uncommon and restricted to the barrens communities.

Chamaedaphne calyculata: Very common in the black spruce and dwarf laurel dwarf scrub and in the peatmoss and reindeer moss bogs; common in the american larch scrub, in the ericaceous dwarf scrub and in the sedge meadows; uncommon in the black spruce scrub and in the creek bed communities.

Gaultheria hispidula: Very common in the black spruce scrub; common in the american larch scrub; uncommon in the second growth forests of balsam fir, in the homogenous second growth scrub of balsam fir and in the black spruce and dwarf laurel dwarf scrub; rare in the wind shaped balsam fir and white spruce scrub and in the ericaceous dwarf scrub.

Kalmia angustifolia: Very common in the black spruce and dwarf laurel dwarf scrub, in the ericaceous dwarf scrub and in the peatmoss and reindeer moss bogs; common in the black spruce scrub; uncommon in the second growth forests of balsam fir, in the american larch scrub, in the sedge meadows and in the barrens communities.

Kalmia polifolia: Very common in the peatmoss and reindeer moss bogs; common in the black spruce and dwarf laurel dwarf scrub, ericaceous dwarf scrub and in the sedge meadows; uncommon in the black spruce scrub, in the american larch scrub and in the barrens communities.

Ledum groenlandicum: Very common in the black spruce scrub, in the american larch scrub, in the black spruce and dwarf laurel dwarf scrub, in the ericaceous dwarf scrub and in the peatmoss and reindeer moss bogs; common in the sedge meadows; uncommon in the barrens communities.

Loiseleuria procumbens: Uncommon and restricted to the barrens communities.

Rhododendron canadense: Very common in the ericaceous dwarf scrub; uncommon in the black spruce scrub, in the creek bed communities, in the black spruce and dwarf laurel dwarf scrub and in the barrens communities.

Vacciniaceae

Gaylussacia baccata: Rare in the ericaceous dwarf scrub.

Gaylussacia dumosa: Uncommon in the peatmoss and reindeer moss bogs.

Vaccinium angustifolium: Very common in the black spruce and dwarf laurel dwarf scrub and in the ericaceous dwarf scrub; common in the black spruce scrub and in the peatmoss and reindeer moss bogs; uncommon in the homogenous second growth scrub of balsam fir, in the creek bed communities, in the sedge meadows and in the barrens communities.

Vaccinium macrocarpon: Uncommon in the sedge meadows and in the tidal flat communities; also found around the ponds of peatmoss and reindeer moss bogs.

Vaccinium oxycoccos: Very common in the american larch scrub, in the peatmoss and reindeer moss bogs and in the sedge meadows; common in the black spruce scrub and in the black spruce and dwarf laurel dwarf scrub; uncommon in the ericaceous dwarf scrub and in the mosaic

of herbaceous plant communities along the seashore and the inlets.

Vaccinium uliginosum: Common in the peatmoss and reindeer moss bogs and in the barrens communities; uncommon in the ericaceous dwarf scrub, in the sedge meadows and in the mosaic of herbaceous plant communities along the seashore and the inlets; rare in the black spruce and dwarf laurel dwarf scrub.

Vaccinium vitis-idaea: Very common in the black spruce and dwarf laurel dwarf scrub and in the ericaceous dwarf scrub; common in the black spruce scrub; uncommon in the peatmoss and reindeer moss bogs, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the barrens communities; rare in the second growth forests of balsam fir.

Pyrolaceae

Moneses uniflora: Uncommon in the second growth forests of balsam fir, in the american larch scrub, in the wind shaped balsam fir and white spruce scrub, in the homogenous second growth scrub of balsam fir and in the heterogenous second growth scrub of balsam fir and deciduous shrubs.

Pyrola asarifolia: More or less common in the american larch scrub; uncommon in the creek bed communities.

Pyrola minor: Uncommon in the second growth forests of balsam fir and in the heterogenous second growth scrub of balsam fir and deciduous shrubs.

Pyrola secunda: Uncommon in the second growth forests of balsam fir, in the black spruce scrub and in the american larch scrub.

Monotropaceae

Monotropa hypopithys: Rare in the second growth forests of balsam fir.

Monotropa uniflora: More or less common in the second growth forests of balsam fir; uncommon in the wind shaped balsam fir and white spruce scrub, in the heterog-

enous second growth scrub of balsam fir and deciduous shrubs, in the white birch scrub, and in the creek bed communities; rare in the black spruce scrub.

Empetraceae

Empetrum eamesii: Uncommon in the barrens communities.

Empetrum nigrum: Very common in the black spruce and dwarf laurel dwarf scrub and in the peatmoss and reindeer moss bogs; common in the ericaceous dwarf scrub and in the sedge meadows; uncommon in the black spruce scrub, in the rocky cliff communities, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the barrens communities.

Diapensiaceae

Diapensia lapponica: Uncommon, but locally abundant, in the barrens communities.

Primulaceae

Glaux maritima: Rare in the peatmoss and reindeer moss bogs; uncommon in the tidal flat communities.

Lysimachia terrestris: Uncommon in the aquatic communities.

Primula laurentiana: Uncommon in the rocky cliff communities and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Primula mistassinica: Rare but locally abundant in an american larch scrub.

Trientalis borealis: Common in the second growth forests of balsam fir, in the american larch scrub, in the ericaceous dwarf scrub, in the peatmoss and reindeer moss bogs and in the sedge meadow; more or less common in the black spruce scrub; uncommon in the homogenous second growth scrub of balsam fir, in the heterogenous second growth scrub of balsam fir and deciduous shrubs, in the white birch scrub, in the creek bed communities, in the mosaic of herbaceous plant communities along the

seashore and the inlets and in the barrens communities; rare in the black spruce and dwarf laurel dwarf scrub and in the wind shaped balsam fir and white spruce scrub.

Grossulariaceae

Ribes glandulosum: Uncommon in the homogenous second growth scrub of balsam fir, in the heterogenous second growth scrub of balsam fir and deciduous shrubs, in the white birch scrub and in the creek bed communities; rare in the second growth forests of balsam fir.

Ribes lacustre: Uncommon in the second growth forests of balsam fir, in the black spruce scrub, in the heterogenous second growth scrub of balsam fir and deciduous shrubs, in the white birch scrub and in the creek bed communities.

Ribes triste: Uncommon in the black spruce scrub, in the heterogenous second growth scrub of balsam fir and deciduous shrubs and in the creek bed communities.

Crassulaceae

Sedum rosea: Uncommon but locally abundant in the rocky cliff communities.

Saxifragaceae

Mitella nuda: Very common in the american larch scrub; more or less common in the black spruce scrub; uncommon in the white birch scrub and in the creek bed communities; rare in the second growth forests of balsam fir.

Saxifraga aizoön: Rare. Found in a rocky cliff community, along the shoreline of the forebay of Western Brook Pond.

Saxifraga cespitosa: Rare and restricted to rocky cliff communities.

Parnassiaceae

Parnassia parviflora: Rare and restricted to rocky cliff communities.

Rosaceae

Agrimonia striata: Found along the roadside, at Shallow Bay.

Alchemilla filicaulis: Found on a gravelly outwash, along Stag River.

Amelanchier bartramiana: Uncommon in the black spruce scrub, in the american larch scrub and in the ericaceous dwarf scrub; rare in the black spruce and dwarf laurel dwarf scrub.

Amelanchier laevis: Uncommon to rare in the black spruce and dwarf laurel dwarf scrub.

Amelanchier spicata: Uncommon in the ericaceous dwarf scrub; rare in the second growth forests of balsam fir.

Fragaria virginiana: Uncommon in the rocky cliff communities, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the cleared areas.

Geum macrophyllum: Uncommon in the american larch scrub and in the creek bed communities.

Geum rivale: Uncommon in the black spruce scrub, in the american larch scrub and in the creek bed communities.

Potentilla anserina: Uncommon in the rocky cliff communities, in the mosaic of herbaceous plant communities along the seashore and the inlets, in the tidal flat communities and in the cleared areas.

Potentilla egedei: Uncommon along the sandy seashores.

Potentilla fruticosa: Common in the american larch scrub; uncommon in the sedge meadows and in the creek bed communities.

Potentilla palustris: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets and in the small creeks.

Potentilla norvegica: Uncommon in the cleared areas.

Potentilla tridentata: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets and in the barrens communities.

Prunus virginiana: Uncommon in the heterogenous second growth scrub of balsam fir and deciduous shrubs and in the creek bed communities.

Pyrus americana: Uncommon to rare, on the dunes of Western Brook, in a balsam fir, white spruce and green alder formation. Rarely found in the second growth forests of balsam fir.

Pyrus decora: Common in the second growth forests of balsam fir; uncommon in the black spruce scrub, in the creek bed communities, in the homogenous second growth scrub of balsam fir, in the heterogenous second growth scrub of balsam fir and deciduous shrubs, in the white birch scrub and in the barrens communities.

Pyrus melanocarpa: Common in the ericaceous dwarf scrub, in the peatmoss and reindeer moss bogs and in the sedge meadows; rare in the creek bed communities.

Rosa nitida: Uncommon in the black spruce scrub, in the creek bed communities and in the sedge meadows; rare in the black spruce and dwarf laurel dwarf scrub and in the american larch scrub.

Rubus acaulis: Uncommon to rare in the mosaic of herbaceous plant communities along the seashore and the inlets.

Rubus chamaemorus: Very common in the black spruce and dwarf laurel dwarf scrub and in the peatmoss and reindeer moss bogs; common in the ericaceous dwarf scrub; more or less common in the black spruce scrub; uncommon in the sedge meadows.

Rubus idaeus: Common in the heterogenous second growth scrub of balsam fir and deciduous shrubs; uncommon in the homogenous second growth scrub of balsam fir, in the creek bed communities, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the cleared areas.

Rubus pubescens: Common in the black spruce scrub and in the american larch scrub; uncommon in the second growth forests of balsam fir, in the heterogenous second growth scrub of balsam fir and deciduous shrubs, in the white birch scrub, in the creek bed communities and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Sanguisorba canadensis: Common in the american larch scrub and in the creek bed communities; uncommon in the black spruce scrub, in the white birch scrub, in the black spruce and dwarf laurel dwarf scrub, in the sedge meadows, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the tidal flat communities.

Spiraea latifolia: Common in the creek bed communities; uncommon in the black spruce scrub, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the tidal flat communities.

Fabaceae

Lathyrus japonicus: Uncommon in the rocky cliff communities and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Lathyrus palustris: Uncommon in the rocky cliff communities, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the tidal flat communities.

Trifolium pratense: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets and in the cleared areas.

Trifolium repens: Uncommon in the rocky cliff communities and in the cleared areas.

Vicia cracca: Uncommon in the cleared areas.

Droseraceae

Drosera anglica: Uncommon in the sedge meadows.

Drosera intermedia: Rare to uncommon in the wet depressions of the peat moss and reindeer moss bogs.

Drosera linearis: Very rare in the peat moss and reindeer moss bogs. Found south of Bakers Brook.

Drosera rotundifolia: Very common in the peat moss and reindeer moss bogs and in the sedge meadows; common in the american larch scrub; uncommon in the black spruce scrub and in the black spruce and dwarf laurel dwarf scrub; rare in the ericaceous dwarf scrub.

Onagraceae

Circaea alpina: Uncommon in the wind shaped balsam fir and white spruce scrub, in the heterogenous second growth scrub of balsam fir and deciduous shrubs, in the creek bed communities and in the rocky cliff communities.

Epilobium angustifolium: Uncommon in the black spruce scrub; uncommon but locally abundant in the cleared areas.

Epilobium alpinum: Found on the western shore of Western Brook Pond.

Epilobium glandulosum: Uncommon in the american larch scrub, in the rocky cliff communities and in the cleared areas; rare in the creek bed communities.

Epilobium latifolium: Very rare in the sandy seashore and lake communities. A large colony was found at the mouth of Stag River.

Epilobium palustre: More or less common in the american larch scrub; uncommon in the creek bed communities, in the rocky cliff communities, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the tidal flat communities.

Myriophyllaceae

Myriophyllum alterniflorum: Uncommon in the aquatic communities.

Myriophyllum tenellum: Uncommon in the aquatic communities.

Hippuridaceae

Hippuris vulgaris: Uncommon to rare in small creeks.

Aceraceae

Acer rubrum: Very rare. A few individuals have been found in a black spruce scrub, south of Bakers Brook.

Acer spicatum: More or less common in the second growth forests of balsam fir; common in the heterogenous second growth scrub of balsam fir and deciduous shrubs; un-

common in the black spruce scrub, in the american larch scrub and in the creek bed communities.

Balsaminaceae

Impatiens capensis: Common in the creek bed communities; uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets.

Cornaceae

Cornus canadensis: Very common in the ericaceous dwarf scrub; common in the second growth forests of balsam fir and in the black spruce scrub; uncommon in the american larch scrub, in the homogenous second growth scrub of balsam fir, in the heterogenous second growth scrub of balsam fir and deciduous shrubs, in the creek bed communities, in the black spruce and dwarf laurel dwarf scrub, in the peatmoss and reindeer moss bogs, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the barrens communities.

Cornus stolonifera: Common in the creek bed communities; uncommon in the black spruce scrub, in the american larch scrub, in the heterogenous second growth scrub of balsam fir and deciduous shrubs and in the white birch scrub.

Cornus suecica: Uncommon to rare. Found on an exposed rocky peninsula colonized by a krummholz of balsam fir, on the north shore of the St. Pauls Inlet.

Araliaceae

Aralia nudicaulis: Uncommon in the creek bed communities; rare in the second growth forests of balsam fir.

Apiaceae

Angelica atropurpurea: More or less common in the american larch scrub; uncommon in the creek bed communities.

Carum carvi: Uncommon in the cleared areas.

Conioselinum chinense: Uncommon in the black spruce scrub, in the american larch scrub, in the creek bed communities, in the rocky cliff communities and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Heracleum maximum: Uncommon in the black spruce scrub, in the white birch scrub, in the creek bed communities, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the cleared areas.

Ligusticum scothicum: Uncommon in the rocky cliff communities and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Aquifoliaceae

Nemopanthus mucronata: Uncommon in the second growth forests of balsam fir, in the black spruce scrub, in the homogenous second growth scrub of balsam fir, in the creek bed communities, in the black spruce and dwarf laurel dwarf scrub and in the ericaceous dwarf scrub; rare in the peatmoss and reindeer moss bogs.

Rhamnaceae

Rhamnus alnifolia: Common in the american larch scrub; uncommon in the creek bed communities; rare in the black spruce scrub.

Santalaceae

Comandra richardsiana: Very rare in the peat moss and reindeer moss bogs. Found south of St. Pauls.

Geocaulon lividum: Uncommon in the black spruce and dwarf laurel dwarf scrub.

Elaeagnaceae

Shepherdia canadensis: Uncommon to rare in the rocky cliff communities; found also in a small stand of krummholz near the mouth of Western Brook.

Caprifoliaceae

Linnaea borealis: Common in the second growth forests of balsam fir, in the black spruce scrub and in the american

larch scrub; uncommon in the homogenous second growth scrub of balsam fir, in the creek bed communities, in the black spruce and dwarf laurel dwarf scrub and in the sedge meadows; rare in the wind shaped balsam fir and white spruce scrub.

Lonicera villosa: Common in the sedge meadows; uncommon in the black spruce scrub, in the american larch scrub, in the homogenous second growth scrub of balsam fir, in the creek bed communities, in the peatmoss and reindeer moss bogs and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Sambucus pubens: Uncommon but locally abundant along the roadside, south of Bakers Brook.

Viburnum cassinoides: Uncommon in the black spruce scrub, in the homogenous second growth scrub of balsam fir, in the creek bed communities, in the black spruce and dwarf laurel dwarf scrub and in the ericaceous dwarf scrub; rare in the second growth forests of balsam fir.

Viburnum edule: Uncommon in the white birch scrub; rare in the black spruce scrub.

Viburnum trilobum: Uncommon in the creek bed communities; rare in the second growth forests of balsam fir.

Gentianaceae

Gentiana nesophila: Uncommon in the rocky cliff communities; uncommon to rare in the mosaic of herbaceous plant communities along the seashore and the inlets.

Halenia deflexa: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets.

Lomatogonium rotatum: Uncommon to rare. Found on a trail at St. Pauls.

Menyanthaceae

Menyanthes trifoliata: Common in the sedge meadows; uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets; rare in the creek bed communities.

Rubiaceae

Galium asprellum: More or less common in the creek bed communities.

Galium kamtschaticum: Rare in the black spruce scrub.

Galium labradoricum: Very common in the american larch scrub; common in the creek bed communities; uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets.

Galium palustre: Uncommon in the tidal flat communities.

Galium trifidum: Uncommon in the creek bed communities.

Galium triflorum: Uncommon in the black spruce scrub, in the heterogenous second growth scrub of balsam fir and deciduous shrubs, in the white birch scrub and in the creek bed communities.

Convolvulaceae

Convolvulus sepium: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets.

Boraginaceae

Mertensia maritima: Uncommon in the rocky cliff communities; found all along the seashore.

Myosotis laxa: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets.

Scrophulariaceae

Castilleja septentrionalis: Rare, found under a white spruce scrub, at the mouth of Western Brook.

Euphrasia: This is a very complex genus. Uncommon in the rocky cliff communities, in the mosaic of herbaceous plant communities along the seashore and the inlets, in the tidal flat communities and in the cleared areas.

Mimulus moschatus: Uncommon to rare, found on a trail near Berry Hill.

Pedicularis palustris: Rare in the sedge meadows, found also along the road.

Rhinanthus crista-galli: Uncommon in the american larch scrub, in the rocky cliff communities, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the cleared areas.

Veronica americana: Uncommon to rare, found along a trail, in an american larch scrub, at Cow Head.

Veronica serpyllifolia: Along the roadside, on a dry gravelly shoulder, at Green Point.

Lentibulariaceae

Pinguicula vulgaris: Uncommon in the sedge meadows, in the rocky cliff communities and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Utricularia cornuta: Uncommon in the sedge meadows and in the wet depressions of the peatmoss and reindeer moss bogs.

Utricularia intermedia: Uncommon in the sedge meadows and in the aquatic communities.

Utricularia minor: Uncommon in the sedge meadows, in the aquatic communities and in the wet depressions of the peatmoss and reindeer moss bogs.

Utricularia vulgaris: Uncommon in the aquatic communities.

Plantaginaceae

Littorella americana: Rare to uncommon in the aquatic communities.

Plantago juncoides: Common to uncommon in the rocky cliff communities; uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets, in the tidal flat communities and in the cleared areas.

Plantago major: Uncommon in the rocky cliff communities, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the cleared areas.

Plantago oliganthos: Uncommon in the tidal flat communities.

Lamiaceae

Galeopsis tetrahit: Uncommon in the cleared areas.

Lycopus americanus: Rare in the creek bed communities.

Lycopus uniflorus: Uncommon in the creek bed communities, in the sedge meadows and in the aquatic communities.

Mentha arvensis: Uncommon in the creek bed communities.

Prunella vulgaris: Uncommon in the american larch scrub and in the cleared areas.

Scutellaria epilobiifolia: Uncommon in the creek bed communities.

Scutellaria lateriflora: Uncommon in the creek bed communities.

Callitrichaceae

Callitriche hermaphroditica: Uncommon to rare in the small streams.

Campanulaceae

Campanula rotundifolia: Uncommon in the sedge meadows, in the rocky cliff communities and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Lobeliaceae

Lobelia dortmanna: Uncommon to rare in the aquatic communities.

Lobelia kalmii: Rare, found in a wet depression within a cleared area, just north of Rocky Harbour.

Asteraceae

Achillea millefolium: Uncommon in the rocky cliff communities, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the cleared areas.

Anaphalis margaritacea: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets and in the cleared areas.

Antennaria spathulata: Rare. Found in a rocky cliff community, along the shoreline of the forebay of Western Brook Pond.

Aster foliaceus: More or less common in the american larch scrub; uncommon in the creek bed communities, in the rocky cliff communities, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the tidal flat communities.

Aster nemoralis: Common in the sedge meadows; uncommon in the aquatic communities and in the wet depressions of the peatmoss and reindeer moss bogs.

Aster puniceus: Common in the creek bed communities; uncommon in the black spruce scrub, in the white birch scrub, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the tidal flat communities.

Aster radula: Common in the american larch scrub and in the sedge meadows; uncommon in the black spruce scrub, in the creek bed communities, in the tidal flat communities and in the aquatic communities.

Aster umbellatus: Uncommon in the cleared areas.

Chrysanthemum leucanthemum: Uncommon to common in the cleared areas.

Cirsium arvense: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets and in the cleared areas; rare in the black spruce scrub.

Cirsium muticum: Uncommon to rare in the creek bed communities.

Eupatorium maculatum: Uncommon in the creek bed communities.

Leontodon autumnalis: Uncommon in the rocky cliff communities, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the cleared areas.

Matricaria matricarioides: Uncommon to rare in the rocky cliff communities; uncommon in the cleared areas.

Prenanthes trifoliolata: Uncommon in the rocky cliff communities.

Senecio aureus: Uncommon in the black spruce scrub, in the american larch scrub and in the creek bed communities.

Senecio pseudo-arnica: Found along the shore of St. Pauls Inlet.

Senecio vulgaris: Uncommon in the rocky cliff communities.

Solidago canadensis: Uncommon on trails.

Solidago macrophylla: Uncommon in the black spruce scrub, in the heterogenous second growth scrub of balsam fir and deciduous shrubs and in the creek bed communities; rare to uncommon in the second growth forests of balsam fir.

Solidago rugosa: Common in the creek bed communities; uncommon in the white birch scrub and in the cleared areas.

Solidago uliginosa: Very common in the american larch scrub; common in the black spruce scrub, in the creek bed communities and in the sedge meadows.

Sonchus arvensis: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets.

Tanacetum vulgare: Found on the roadside, at Martin Point.

Taraxacum officinale: Common to uncommon in the cleared areas; uncommon in the rocky cliff communities and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Alismataceae

Sagittaria graminea: Uncommon to rare in the aquatic communities.

Juncaginaceae

Triglochin gaspense: Uncommon in the tidal flat communities.

Triglochin maritima: Common in the american larch scrub, uncommon in the sedge meadows.

Triglochin palustris: Uncommon in the mosaic of herbaceous plant communities along the seashore and the in-

lets and in the wet depressions of the peatmoss and reindeer moss bogs.

Zosteraceae

Zostera marina: Uncommon to common in the tidal flat communities.

Potamogetonaceae

Potamogeton alpinus: Uncommon but locally abundant in the small streams.

Potamogeton amplifolius: Uncommon to rare in the aquatic communities.

Potamogeton epihydrus: Uncommon in the ponds of the peatmoss and reindeer moss bogs, in the small streams and in the aquatic communities.

Potamogeton filiformis: Uncommon in the tidal flat communities.

Potamogeton gramineus: Uncommon in the aquatic communities.

Potamogeton natans: Uncommon but locally abundant in the small streams.

Ruppiaceae

Ruppia maritima: Uncommon in the tidal flat communities.

Liliaceae

Clintonia borealis: Common in the second growth forests of balsam fir; uncommon in the black spruce scrub, in the heterogenous second growth scrub of balsam fir and deciduous shrubs and in the creek bed communities.

Maianthemum canadense: Common in the second growth forests of balsam fir and in the ericaceous dwarf scrub; uncommon in the black spruce scrub, in the wind shaped balsam fir and white spruce scrub, in the heterogenous second growth scrub of balsam fir and deciduous shrubs, in the white birch scrub, in the creek bed communities, in the peatmoss and reindeer moss bogs, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the barrens communities.

Smilacina stellata: Uncommon in the creek bed communities, in the rocky cliff communities, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the dunes and sandy seashore communities.

Smilacina trifolia: Very common in the black spruce scrub and in the american larch scrub; common in the creek bed communities, in the black spruce and dwarf laurel dwarf scrub and in the sedge meadows; uncommon in the ericaceous dwarf scrub, in the peatmoss and reindeer moss bogs, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the barrens communities.

Streptopus amplexifolius: Uncommon to rare in the second growth forests of balsam fir, in the heterogenous second growth scrub of balsam fir and deciduous shrubs and in the creek bed communities.

Streptopus roseus: Uncommon to rare in the second growth forests of balsam fir and in the creek bed communities.

Tofieldia glutinosa: Uncommon in the american larch scrub and in the sedge meadows.

Trilliaceae

Trillium cernuum: Rare in the creek bed communities.

Iridaceae

Iris hookeri: Uncommon but locally abundant in the rocky cliff communities and in the mosaic of herbaceous plant communities along the seashore and the inlets; uncommon in the tidal flat communities.

Iris versicolor: Common in the american larch scrub and in the creek bed communities; uncommon but locally abundant in the mosaic of herbaceous plant communities along the seashore and the inlets; uncommon in the sedge meadows and in the tidal flat communities.

Sisyrinchium montanum: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets.

Orchidaceae

Arethusa bulbosa: Uncommon in the sedge meadows and in the peatmoss and reindeer moss bogs.

Calopogon pulchellus: Uncommon to rare in the peatmoss and reindeer moss bogs.

Corallorhiza maculata: Rare in the second growth forests of balsam fir, at Berry Hill.

Cypripedium acaule: Rare, found in a dry creek bed near Berry Hill.

Cypripedium calceolus: Rare in the black spruce scrub, found near Berry Hill.

Cypripedium reginae: Uncommon in the american larch scrub.

Goodyera repens: Uncommon in the second growth forests of balsam fir.

Goodyera tesselata: Uncommon in the second growth forests of balsam fir and in the heterogenous second growth scrub of balsam fir and deciduous shrubs.

Habenaria clavellata: Rare in the sedge meadows.

Habenaria dilatata: Common in the american larch scrub; uncommon in the black spruce scrub, in the creek bed communities and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Habenaria hyperborea: Uncommon in the american larch scrub.

Habenaria obtusata: More or less common in the second growth forests of balsam fir; uncommon in the black spruce scrub, in the homogenous second growth scrub of balsam fir and in the wind shaped balsam fir and white spruce scrub.

Habenaria orbiculata: Rare in the second growth forests of balsam fir.

Habenaria psycodes: Uncommon to rare in the mosaic of herbaceous plant communities along the seashore and the inlets and in the creek bed communities.

Listera convallarioides: Uncommon in the black spruce scrub and in the american larch scrub.

Listera cordata: More or less common in the second growth forests of balsam fir; uncommon in the black spruce scrub and in the american larch scrub.

Malaxis unifolia: Uncommon to rare in the american larch scrub and in the sedge meadows.

Pogonia ophioglossoides: Uncommon in the sedge meadows.

Spiranthes romanzoffiana: Found on a wet sloping trail, at St. Pauls.

Juncaceae

Juncus articulatus: Rare in the american larch scrub.

Juncus balticus: Uncommon in the tidal flat communities.

Juncus brevicaudatus: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets, in the tidal flat communities and in the cleared areas.

Juncus bufonius: Uncommon in the heterogenous second growth scrub of balsam fir and deciduous shrubs.

Juncus canadensis: Uncommon in the american larch scrub.

Juncus effusus: Uncommon in the cleared areas.

Juncus filiformis: Uncommon in the american larch scrub and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Juncus pelocarpus: Uncommon in the aquatic communities and in the flashets of the peatmoss and reindeer moss bogs.

Juncus stygius: Rare in the sedge meadows.

Juncus tenuis: Uncommon in the heterogenous second growth scrub of balsam fir and deciduous shrubs.

Juncus trifidus: Uncommon in the barrens communities.

Luzula multiflora: Uncommon in the heterogenous second growth scrub of balsam fir and deciduous shrubs and in the cleared areas.

Luzula spicata: Rare. Found in a rocky cliff community, along the shoreline of the forebay of Western Brook Pond.

Cyperaceae

Carex angustior: Found on a logging trail at Sally Cove.

Carex aquatilis: Uncommon but locally abundant in the creek bed communities; uncommon in the american larch scrub, in the peatmoss and reindeer moss bogs and in the sedge meadows.

Carex atratiformis: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets.

Carex aurea: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets.

Carex brunnescens: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets and in the creek bed communities.

Carex buxbaumii: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets and in the creek bed communities.

Carex canescens: Uncommon in the american larch scrub, in the creek bed communities, in the mosaic of herbaceous plant communities along the seashore and the inlets and in the tidal flat communities.

Carex capillaris: Uncommon in the rocky cliff communities and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Carex cephalantha: Uncommon in the wet depressions of the peatmoss and reindeer moss bogs.

Carex chordorrhiza: Rare in the sedge meadows.

Carex crawei: Rare in the dunes and sandy seashore communities.

Carex deweyana: Uncommon to rare in the cleared areas.

Carex diandra: Uncommon in the american larch scrub.

Carex disperma: Uncommon in the black spruce scrub and in the american larch scrub; rare in the creek bed communities.

Carex exilis: Very common in the sedge meadows; uncommon in the american larch scrub and in the peatmoss and reindeer moss bogs.

Carex flava: Uncommon in the creek bed communities.
Carex gracillima: Found on a logging trail, near Berry Hill.
Carex gynocrates: Uncommon in the american larch scrub and in the sedge meadows; rare in the ericaceous dwarf scrub.
Carex interior: Very common in the american larch scrub; uncommon in the black spruce scrub, in the creek bed communities and in the tidal flat communities.
Carex intumescens: Uncommon in the creek bed communities.
Carex lasiocarpa: Very common in american larch scrub; common in the sedge meadows; uncommon in the black spruce scrub and in the creek bed communities.
Carex lepidocarpa: Uncommon in the american larch scrub.
Carex leptalea: Common in the american larch scrub and in the creek bed communities; uncommon in the black spruce scrub.
Carex leptonervia: Uncommon in the creek bed communities and in the mosaic of herbaceous plant communities along the seashore and the inlets.
Carex limosa: Common in the sedge meadows; uncommon in the american larch scrub, in the mosaic of herbaceous plant communities along the seashore and the inlets, in the tidal flat communities and the wet depressions of the peatmoss and reindeer moss bogs.
Carex livida: Common in the american larch scrub and in the sedge meadows.
Carex mackenziei: Uncommon in the tidal flat communities.
Carex michauxiana: Found on a wet muddy edge of a pond, near Berry Hill.
Carex miliaris: Uncommon in the dunes and sandy seashore communities.
Carex nigra: Uncommon in the rocky cliff communities. Uncommon but locally abundant in the mosaic of herbaceous plant communities along the seashore and the inlets and in the cleared areas.
Carex oligosperma: Found on a wet trail near Western Brook Pond.

Carex paleacea: Uncommon in the tidal flat communities.

Carex pallescens: Found on a logging trail at Sally Cove.

Carex pauciflora: Uncommon in the sedge meadows; rare in the black spruce and dwarf laurel dwarf scrub and in the ericaceous dwarf scrub.

Carex paupercula: Uncommon in the black spruce scrub, in the american larch scrub and in the creek bed communities.

Carex pieperiana: Uncommon in the american larch scrub.

Carex projecta: Found on a logging trail, north of St. Pauls Inlet.

Carex rariflora: Common in the peatmoss and reindeer moss bogs; uncommon in the sedge meadows.

Carex recta: Uncommon in the creek bed communities and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Carex rostrata: Uncommon in the black spruce scrub, in the american larch scrub, in the creek bed communities, in the sedge meadows, in the aquatic communities and in the wet depressions of the peatmoss and reindeer moss bogs.

Carex rupestris: Uncommon in the sedge meadows.

Carex salina: Uncommon but locally abundant in the tidal flat communities.

Carex scoparia: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets, in the tidal flat communities and in the heterogenous second growth scrub of balsam fir and deciduous shrubs.

Carex stipata: Uncommon in the creek bed communities and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Carex tenuiflora: Uncommon in the american larch scrub.

Carex trisperma: Very common in the black spruce scrub; uncommon in the american larch scrub, in the creek bed communities, in the black spruce and dwarf laurel dwarf scrub, in the ericaceous dwarf scrub and in the cleared areas; rare in the second growth forests of balsam fir and in the wind shaped balsam fir and white spruce scrub.

Carex vaginata: Uncommon in the black spruce scrub and in the american larch scrub.

Carex vesicaria: Found on a logging trail, north of St. Pauls Inlet.

Carex viridula: Found on the roadside, near Western Brook, and on a trail, at St. Pauls.

Carex viridula × lepidocarpa: Found on a wet trail, at Cow Head.

Eleocharis halophila: Uncommon in the tidal flat communities.

Eleocharis palustris: Uncommon but locally abundant in the aquatic communities.

Eleocharis smallii: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets.

Eriophorum angustifolium: Common in the american larch scrub; more or less common in the sedge meadows; uncommon in the black spruce and dwarf laurel dwarf scrub, in the ericaceous dwarf scrub and in the peatmoss and reindeer moss bogs.

Eriophorum chamissonis: Uncommon, in the wet depressions of the peatmoss and reindeer moss bogs.

Eriophorum gracile: Uncommon in the wet depressions of the peatmoss and reindeer moss bogs.

Eriophorum spissum (incl.: *Eriophorum pylaieanum* Raymond): More or less common in the black spruce and dwarf laurel dwarf scrub; uncommon in the ericaceous dwarf scrub and in the peatmoss and reindeer moss bogs; rare in the black spruce scrub and in the sedge meadows.

Eriophorum virginicum: Uncommon to rare in the peatmoss and reindeer moss bogs.

Eriophorum viridi-carinatum: Uncommon to rare in the black spruce scrub.

Rhynchospora alba: Uncommon in the sedge meadows, uncommon but locally abundant in the wet depressions of the peatmoss and reindeer moss bogs.

Scirpus acutus: Uncommon in the tidal flat communities, uncommon but locally abundant in the aquatic communities.

Scirpus americanus: Uncommon in the tidal flat communities.

Scirpus atrocinctus: Uncommon to rare in the creek bed communities.

Scirpus cespitosus: Very common in the peatmoss and reindeer moss bogs and in the sedge meadows; common in the american larch scrub; uncommon in the black spruce and dwarf laurel dwarf scrub and in the ericaceous dwarf scrub.

Scirpus hudsonianus: Uncommon in the american larch scrub and in the sedge meadows.

Scirpus rufus: Uncommon in the tidal flat communities.

Scirpus subterminalis: Uncommon in the aquatic communities.

Eriocaulaceae

Eriocaulon septangulare: Uncommon to rare in the aquatic communities and in the sedge meadows.

Poaceae

Agropyron repens: Uncommon in the cleared areas.

Agropyron trachycaulum: Uncommon in the american larch scrub.

Agrostis alba: Common in the mosaic of herbaceous plant communities along the seashore and the inlets and in the cleared areas; uncommon in the rocky cliff communities and in the tidal flat communities.

Agrostis scabra: Common in the american larch scrub.

Agrostis tenuis: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets.

Ammophila breviligulata: Very common in the dunes and sandy seashore communities, uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets.

Anthoxanthum odoratum: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets.

Bromus ciliatus: More or less common in the american larch scrub, uncommon in the creek bed communities.

Calamagrostis canadensis: Common in the creek bed communities and in the sedge meadows; uncommon in the black spruce scrub, in the ericaceous dwarf scrub, in the peatmoss and reindeer moss bogs, in the mosaic of herbaceous plant communities along the seashore and the inlets, in the cleared areas and in the aquatic communities.

Catabrosa aquatica: Found on the tilted breccia at White Rock Islets.

Cinna latifolia: Uncommon in the creek bed communities.

Deschampsia flexuosa: Uncommon in the american larch scrub; uncommon to common in the mosaic of herbaceous plant communities along the seashore and the inlets.

Elymus arenarius: Uncommon in the rocky cliff communities and in the dunes and sandy seashore communities.

Festuca rubra: Common in the mosaic of herbaceous plant communities along the seashore and the inlets and in the cleared areas; uncommon but locally abundant in the rocky cliff communities; uncommon in the american larch scrub, in the creek bed communities and in the tidal flat communities.

Glyceria borealis: Found on a wet trail, at Cow head.

Glyceria canadensis: Uncommon in the creek bed communities.

Glyceria striata: Common in the creek bed communities; uncommon in the black spruce scrub, in the white birch scrub and in the sedge meadows.

Hordeum jubatum: Uncommon to rare in the tidal flat communities.

Milium effusum: Rare in the creek bed communities.

Muhlenbergia glomerata: Uncommon in the american larch scrub.

Phleum pratense: Uncommon in the mosaic of herbaceous plant communities along the seashore and the inlets and in the cleared areas.

Poa alpina: Rare. Found in a rocky cliff community, along the shoreline of the forebay of Western Brook Pond.

Poa eminens: Found on the tilted breccia, at St. Pauls.

Poa palustris: Uncommon in the creek bed communities, in the rocky cliff communities and in the mosaic of herbaceous plant communities along the seashore and the inlets.

Poa pratensis: Common in the mosaic of herbaceous plant communities along the seashore and the inlets and in the cleared areas; uncommon in the rocky cliff communities and in the tidal flat communities.

Puccinellia paupercula: Uncommon in the tidal flat communities.

Spartina pectinata: Uncommon in the tidal flat communities.

Trisetum spicatum: Uncommon to rare in the mosaic of herbaceous plant communities along the seashore and the inlets.

Sparganiaceae

Sparganium angustifolium: Uncommon in the aquatic communities.

Sparganium eurycarpum: Found along a stream flowing into Shallow Bay, at Lower Head.

Sparganium minimum: Uncommon in the aquatic communities.

Sparganium multipedunculatum: Found in a flashet within a peatmoss and reindeer moss bog.

Typhaceae

Typha latifolia: Uncommon in the creek bed communities.

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BIBLIOGRAPHY

BAIRD, D. M. 1958. Geology. Sandy Lake (West Half) Newfoundland 1/253,440. Geological Survey of Canada, Map 47-1959.

BLAKE, S. F. 1914. A new *Cochlearia* from Newfoundland. Rhodora **16**: 135-136.

BOUCHARD, A. 1974. The Coastal Plain Vegetation of the Gros Morne National Park. Contract 71-186 with the Department of Indian Affairs and Northern Development, National and Historic Parks Branch, Ottawa, Ontario, Canada, 171 pp.

COTTAM, G., & J. T. CURTIS. 1956. The use of distance measures in phytosociological sampling. Ecology **37**: 451-460.

CURTIS, J. T. 1959. The vegetation of Wisconsin. An Ordination of Plant Communities. The University of Wisconsin Press, 657 pp.

DAMMAN, A. W. H. 1965. The Distribution of Northern and Southern Elements in the Flora of Newfoundland. Rhodora **67**: 363-392.

FERNALD, M. L. 1911. A Botanical Expedition to Newfoundland and Southern Labrador. Rhodora **13**: 109-162.

———. 1918. The contrast in the floras of Eastern and Western Newfoundland. Am. Jour. Bot. **5**: 237-247.

———. 1925. Persistence of plants in unglaciated areas of Boreal America. Mem. Am. Acad. Arts Sci. **15**: 239-342.

———. 1926-27. Two summers of botanizing in Newfoundland. Contr. Gray Herb. **76**.

———. 1933. Recent discoveries in the Newfoundland flora. Contr. Gray Herb. **101**.

———. 1950. Gray's Manual of Botany. American Book Co., New York. 8th ed. 1632 pp.

GRANT, D. R. 1970. Late Pleistocene Re-advance of Piedmont Glaciers in Western Newfoundland. Maritime Sediments **5**: 126-128.

———. 1973. Terrain conditions, Gros Morne National Park, Western Newfoundland. Geol. Surv. Can., Paper 73-1, part B:121-125.

HARE, F. K. 1952. The climate of the Island of Newfoundland. Can. Dep. Mines Tech. Surv., Geogr. Bull. **2**: 36-88.

LEROY, J. F. 1957. Les botanistes français en Amérique du Nord avant 1850. CNRS, Paris, 360 pp.

MAYCOCK, P. F. 1963. The phytosociology of the deciduous forests of extreme southern Ontario. Can. Jour. Bot. **41**: 379-438.

OHMANN, L. F., & R. R. REAM. 1971. Wilderness ecology: virgin plant communities of the Boundary Waters Canoe Area. N. Cent. Forest Exp. Sta., St. Paul, Minn. 55 pp.

ROULEAU, E. 1956. A check-list of the vascular plants of the Province of Newfoundland. Contr. Inst. Bot. Univ. Montréal **69**: 41-106.

————. 1970. Répertoire de l'Index Kewensis et de ses suppléments 1 à 14. Herbier Marie Victorin, Montréal, 370 pp.

WAGHORNE, A. C. 1893. The flora of Newfoundland, Laborador and St. Pierre et Miquelon. Trans. N. S. Inst. Sci. ser 2, **1**: 359-373.

————. 1895. The flora of Newfoundland, Labrador and St. Pierre et Miquelon. Part II. Trans. N. S. Inst. Sci. ser. 2, **2**: 83-100.

————. 1898. The flora of Newfoundland, Labrador and St. Pierre et Miquelon. Part III. Trans. N. S. Inst. Sci. ser. 2, **2**: 361-401.

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ON THE GEOGRAPHICAL DISTRIBUTION, ECOLOGY AND DISTINCTIVE FEATURES OF LISTERA × VELTMANII CASE

PAUL M. CATLING

Until recently the Veltman's hybrid Twayblade (*Listera × veltmanii* Case) was known only from the vicinity of the type locality in Alger Co., Michigan (*Case* 1964a, 1964b). Since both of its putative parents, *L. convallarioides* (Sw.) Nutt. and *L. auriculata* Wieg., grow in close proximity in other parts of the northeast, it seemed likely that the hybrid would occur elsewhere. This prediction was realized on 20 July, 1975, when we discovered *Listera × veltmanii* along the sandy banks of the Pancake River near the Lake Superior shore, Algoma Dist., Ontario. A subsequent search of some major northeastern herbaria (AMES, CAN, DAO, GH, LKHD, NEBC, TRT) revealed that the hybrid, although rare, is widely distributed in northeastern North America (fig. 1). Whenever collected it was confused with either one or the other of its putative parents. Since the ten new and widely separated stations now known, in addition to the type locality, represent the total known distribution of this hybrid, the specimen data are fully cited below.

CANADA: **New Brunswick:** KENT CO.: mountain back of Claire, 17 July 1904, *A. A. Eaton* (AMES 2567). **Newfoundland:** GRAND FALLS DIST.: low alluvial woods, north bank of river below the falls, Grand Falls, valley of Exploits River, 10 July 1911, *M. L. Fernald* and *K. M. Wiegand* 5242 (AMES 84315). ST. GEORGE DIST.: Harry's Brook, Black Duck, 27 June 1930, *Rachel B. Kennedy* (AMES 84265). BONAVISTA SOUTH DIST.: Terra Nova National Park, 14 July 1962, *R. D. Muir* (DAO). **Quebec:** GASPE WEST CO.: alluvial wooded banks, Riviere St. Anne des Monts, 3-17 August 1905, 16 July 1906, *M. L. Fernald* and *J. F. Collins* (AMES 84271, CAN 16751 & 16748). CHARLEVOIX CO.: Ste.-Anne-des-Lacs, Lac Barn, 11 July 1968, *G. Lemieux* 14256 (DAO). **Ontario:** ALGOMA DIST.: cedar swamp near Duck Harbour, vicinity of Michipicoten Harbour, 29 July 1938, *R. C. Hosie et al.* (CAN 16732); cedar swamp at Rahal Lake, vicinity of Michipicoten Harbour, 15 July 1938, *R. C. Hosie et al.* (TRT 55174); in coarse sandy soil along the spring-flooded banks of river under alders, Pancake River near Lake Superior shore, 20 July 1975, *P. M.*

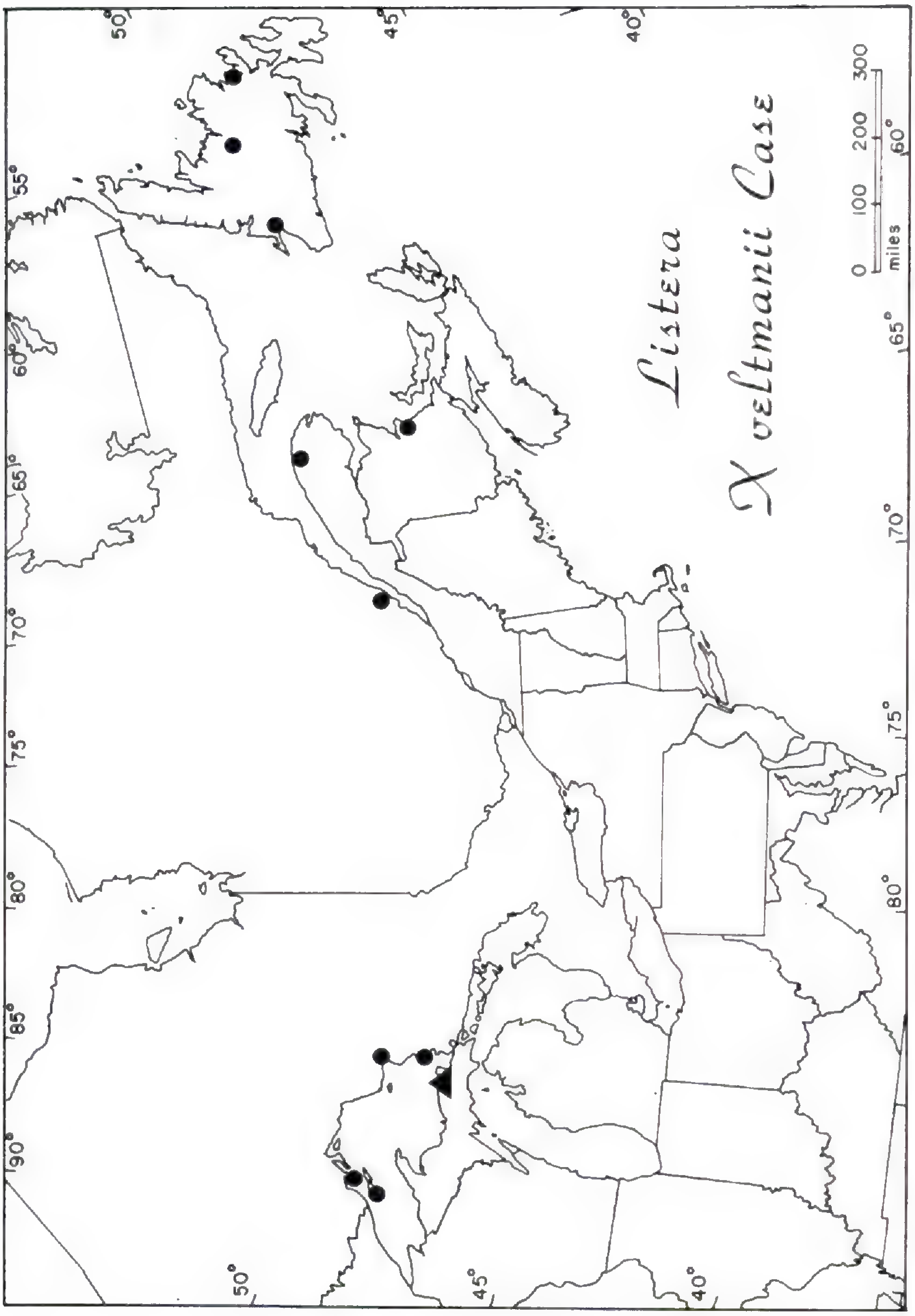

Fig 1. Distribution of *L.* × *veltmanii* Case based on specimens at AMES, CAN, DAO, GH, LKHD, NEBC and TRT. The general area surrounding the type locality is indicated with a solid triangle.

Catling, K. L. McIntosh, and *S. M. McKay* (TRT 181960, 181961, DAO, CAN). THUNDER BAY DIST.: moist boggy soil under cedars, northwest corner of Perry's Bay, Silver Islet, Sibley Penn., 22 July 1950, *C. E. Garton et al.* (AMES 84868, DAO, LKHD 3660, TRT 78051); same as preceding, 6 August 1972, *C. E. Garton* 15163 (LKHD 30858). UNITED STATES: **Michigan:** ISLE ROYALE: mixed open woods, Grace Harbour, 7 July 1930, *C. A. Brown* 3220 (CAN 200860).

Although Case (pers. comm.) reports finding large colonies of intermediate plants at Grand Marais, Michigan, which were clearly not F_1 hybrids, only two sheets were found in the herbaria searched that may have represented backcrosses (with *Listera convallarioides*). On one of these the apparent backcross plants were mounted with some more typical hybrids from Duck Harbour, Ontario (cited above). The other sheet represented a collection from Summit Depot, New Brunswick (on calcareous peat under cedar and tamarack by Loon Lake, Mad. Co., 22 July 1960, *G. C. Cunningham* and *O. L. Loucks,* s.n. (DAO)).

In a few cases the hybrids were found on the same sheet with typical specimens of one of the parents: the specimen of *Listera* × *veltmanii* from Claire, New Brunswick, as well as that from Rahal Lake, Ontario, were mounted on the same sheet with *L. convallarioides,* and hybrids from Harry's Brook, Newfoundland, were mixed with typical *L. auriculata.* In almost all cases one or both putative parents have been collected from the same location as the hybrid. Case (*loc. cit.*) has also reported finding the hybrid in association with either one or the other parent.

At Pancake Bay an ecological separation between the hybrids and the putative parents was apparent. *Listera auriculata* was quite frequent (ca. 100 flowering plants in ¼ mile) on the moist sandy banks of the Pancake River under alders (*Alnus rugosa* (DuRoi) Spreng.) with the primary associates being the mosses *Atrichum oerstedianum* (C. Mull.) Mitt. and *Hypnum lindbergii* Mitt., and the liverwort, *Pellia epiphylla* (L.) Corda. Other frequent associates included *Carex intumescens* Rudge, *Equisetum sylvaticum* L., *Rubus pubescens* Raf., *Viola* cf. *nephrophylla*

Greene, *Onoclea sensibilis* L., *Pyrola minor* L., *Scutellaria lateriflora* L., *Aster lateriflorus* (L.) Britt., and *Streptopus amplexifolius* (L.) DC. var. *denticulatus* Fassett. This is a characteristic habitat and association for *L. auriculata* in Ontario.

Listera convallarioides was not found in the immediate area of the seasonally flooded riverbanks, but about 20-40 metres up some of the intermittent streams in a forest of White Birch (*Betula papyrifera* Marsh). Here it was growing profusely (at least 200 flowering plants) among the sedges in the black mucky soil of a streambed. The sedge community was dominated by *Carex scabrata* Schwein. Other associates included *Carex stipata* Muhl., *Carex intumescens* Rudge, *Eupatorium maculatum* L., *Circaea alpina* L., *Viola* cf. *nephrophylla* Greene, *Aster lateriflorus* (L.) Britt., *Aster umbellatus* Mill., *Veronica americana* (Raf.) Schw., and several bryophytes (*Mnium* spp., etc.).

About thirty flowering plants of *Listera* × *veltmanii* were found along the sandy river banks near plants of *L. auriculata.* At least twenty grew in an apparently more unstable habitat where much sand covered the ground (fig. 2a), and only *Atrichum oerstedianum, Equisetum sylvaticum* and *Carex intumescens* were frequent associates. These habitats sometimes occurred where streams drained into the river from the surrounding forests. Generally the hybrids were found in small, widely scattered groups of one to five plants, and only in a few cases were they in very close association (within a few metres) with *L. auriculata.* To some extent a distinct and perhaps intermediate type of habitat was characteristic of the hybrid, and the hybrid habitat was certainly more disturbed. Case (1964b, p. 71) similarly noted that *L.* × *veltmanii* grew in a habitat "that was not exactly typical of that of either parent", and he also noted "considerable evidence of physical disturbance."

At Pancake Bay all of the plants of *Listera* found could easily be assigned to either *L.* × *veltmanii, L. auriculata,*

Fig. 2. *Listera* × *veltmanii* Case photographed near the mouth of the Pancake River, Algoma Dist., Ontario. a, plant growing in coarse sand near riverbank. b, close-up of flower showing short claw and partial auricle at base of lip.

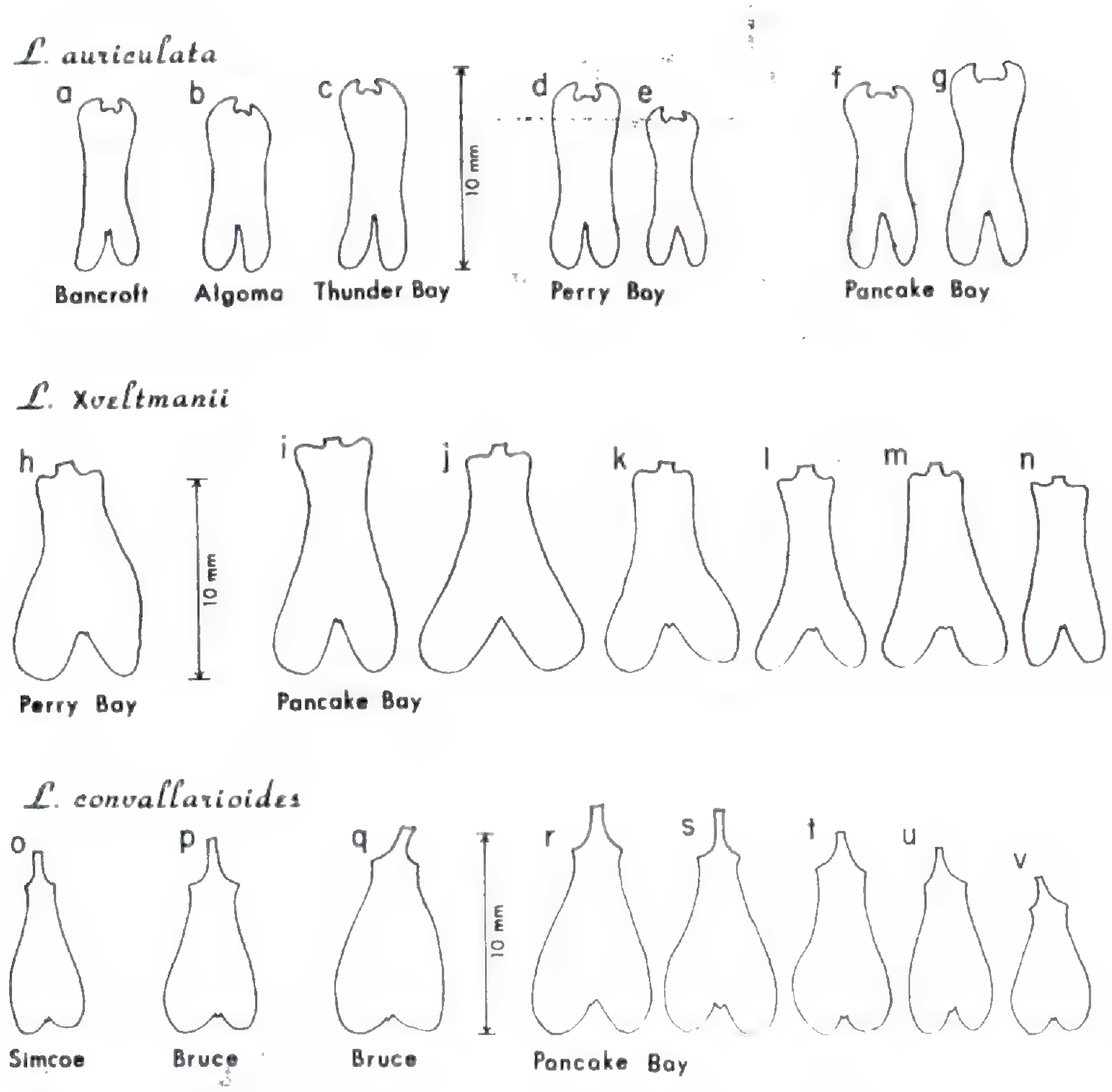

Fig. 3. Camera lucida drawings of the lips of *Listera* spp.

a-g, *Listera auriculata.* a, York R., near Bancroft, Hastings Co., 45°04′, 77°44′ (TRT 181742). b, Michipicoten Harbour, Algoma Dist., 48°00′, 85°00′ (TRT 55177). *c,* Jackfish Lake, 48°45′, 87°15′, Thunder Bay Dist. (TRT 49731). d, e, Perry Bay, Thunder Bay Dist., 48°20′, 88°50′ (TRT 181952). f, g, Pancake Bay, Algoma Dist., 46°57′, 84°41′ (TRT 181957).

h-n, *L.* × *veltmanii.* h, Perry Bay, Sibley Peninsula, Thunder Bay Dist. (TRT 78051). i-n, Pancake Bay, Algoma Dist. (TRT 181960, 181961).

o-v, *L. convallarioides.* o, Bass Lake, Simcoe Co., 44°35′, 79°31′ (TRT 148120). p, Lymburner Lake, Bruce Co., 45°11′, 81°20′ (TRT 161002). q, Cape Croker, Bruce Co., 44°56′, 81°01′ (TRT 38541). r-v, Pancake Bay, Algoma Dist. (TRT 181955).

or *L. convallarioides.* The extremes in variation of lip shape were collected, and are illustrated in figure 3. When these were compared with lip outlines from other stations it became clear that both putative parents and hybrids were quite typical. For instance, *Listera auriculata* from Pancake Bay, and from Perry Bay (where the hybrid has also been found), was quite similar to *L. auriculata* from locations where *L. convallarioides* and the hybrid are unknown (fig. 3a-3c). Similarly *L. convallarioides* from Pancake Bay was comparable with *L. convallarioides* throughout its range including Bruce and Grey Counties, Ontario, where *L. auriculata* and *L.* × *veltmanii* are not known to occur (fig. 3o-3q). This would seem to further establish the rarity of backcrossing.

The lip of *Listera* × *veltmanii* is quite distinctive in having a relatively short claw and in being very slightly auricled at the base (fig. 2b, 3h-3n). *L. auriculata* is almost without a claw and has well developed auricles, while *L. convallarioides* is long-clawed with basal prominences ("teeth"). In addition the lips of *L.* × *veltmanii* and *L. convallarioides* tend to be distally widened (cuneate) whereas *L. auriculata* is often as wide basally as distally, or slightly widened only in the distal third. In *L.* × *veltmanii* the lip tends to have more convex lateral margins while in *L. convallarioides* the lateral margins are concave for at least the distal third of their length. Finally the apical sinus is over 1/5 of the length of the lip in *L.* × *veltmanii* and *L. auriculata,* but usually much less in *L. convallarioides.* It is important to note that some variation in lip shape, especially the apical dilation, is correlated with position of the flower in the raceme. Flowers nearer to the top of the raceme tend to have lips that are less apically dilated than those below. Figures 3m and 3n illustrate this well, since both were taken from the same raceme, fig. 3n representing the terminal (14th) flower while fig. 3m represents the third flower from the base.

Other floral parts have not been quantitatively studied, but intermediacy is apparent in some cases. For instance,

the width of the lateral petals and length of the column of *Listera* × *veltmanii* tend to be intermediate between the putative parents. In length of the floral parts the hybrids are generally closer to *L. convallarioides.* At maturity the ovaries of *L.* × *veltmanii* are similar to *L. convallarioides* in being more ascending and less anteriorly gibbous than *L. auriculata.*

As well as in these floral characters *Listera* × *veltmanii* frequently differs from its putative parents in being much larger (up to 2.5 dm.). Also, in *L.* × *veltmanii* the glandular pubescence of the flower pedicels is generally shorter and more sparse than that of the main axis. In *L. convallarioides* this glandular pubescence is just as thick and long on the pedicels as on the main axis of the raceme, and extends in a somewhat reduced form over the ribs of the ovary. In *L. auriculata* the flower pedicels and ovary are glabrous.

A final interesting distinction concerns flowering time. When we visited the Pancake River on 20 July we found several plants of *Listera* × *veltmanii* in full anthesis, and many plants still had several upper flowers intact, but all plants of *L. auriculata* and *L. convallarioides* were either past anthesis with all of the flowers quite withered, or with only a few of the uppermost flowers intact. Judging from the dates accompanying some herbarium specimens, it would seem that *L.* × *veltmanii* continues flowering somewhat later than its putative parents at other stations as well.

The fact that *Listera* × *veltmanii* is presently known only where the ranges of the putative parents overlap further suggests that Case was correct in assuming the plant to be a hybrid. *Listera auriculata* has a northeastern distribution extending from the Lake Superior region north to Hudson Bay and east to northern New England and the Canadian Maritime Provinces. In the east *L. convallarioides* overlaps with *L. auriculata,* but extends further to the south in New England and in the Great Lakes region. Unlike *L. auriculata* it ranges west across southern Canada

to the Pacific coast and southward in the mountains. In parts of the east where *L. convallarioides* extends further south than *L. auriculata,* no *L.* × *veltmanii* has been found despite the relatively more intensive floristic study of these areas. The absence of *L.* × *veltmanii* outside the region of sympatry of the putative parents therefore seems real.

Although this interesting hybrid is rare, it has likely been overlooked in some areas. Its apparent restriction to the sympatric distribution of the parents, its widespread occurrence, and frequent association with the putative parents, would seem to suggest spontaneous hybridization and low hybrid fertility. The fact that *Listera* × *veltmanii* is frequently quite distinct, and that the putative parents nearby are also quite distinct, suggests that the hybrid is often somehow effectively isolated from its parents.

ACKNOWLEDGEMENTS

I wish to thank Mr. F. W. Case II for verifying the identity of TRT 181960, 181961, 55174, 55175 as *Listera* × *veltmanii.* Dr. R. R. Ireland confirmed the identification of bryophytes. Miss K. L. McIntosh and Miss S. M. McKay were of assistance in the field. Mr. F. W. Case II (Saginaw, Michigan) and Dr. L. A. Garay (Ames Herbarium, Harvard University) are thanked for their critical reading of the manuscript.

LITERATURE CITED

CASE, F. W. 1964a. A hybrid twayblade and its rarer parent, *Listera auriculata,* in northern Michigan. Michigan Botanist, **3**: 67-70.

————. 1964b. Orchids of the western Great Lakes region. Cranbrook Institute of Science, Bloomfield Hills, Michigan. 147 pp.

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THE SARRACENIA RUBRA COMPLEX

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INTRODUCTION AND HISTORY

In his *"Flora Carolinia"*, 1788, Walter described *Sarracenia rubra*. MacFarlane, in his monograph of the *"Sarraceniaceae"* (1908), treated *S. rubra* in a broad sense and did not name any forms or varieties.

In 1929, E. T. Wherry described *Sarracenia jonesii* from Flat Rock, North Carolina, as a separate species closely related to *S. rubra* Walt. According to Wherry, the range of *S. jonesii* extended from the mountains of Henderson and Buncombe Counties, North Carolina, southwestward through Alabama to the coast of western Florida and into eastern Mississippi.

In 1949, C. R. Bell published his "A Cytotaxonomic Study of the *Sarraceniaceae* of North America." In this work, he reduced *Sarracenia jonesii* to the rank of forma under *S. rubra* Walt., including in forma *jonesii* all herbarium specimens from the known range of the entire *S. rubra* complex that showed leaves with sharply expanded upper pitcher tubes.

S. T. McDaniel, in his doctoral thesis (1966), further reduced *Sarracenia jonesii*, considering that it had no taxonomic status.

From the time of Bell's work, botanists and carnivorous plant buffs interested in *Sarracenia* have argued pro and con considering the validity of *S. jonesii* and the nature of *S. rubra*. Almost every discussion appearing in print presents a different view. After much discussion by others, Wherry, in 1972, reduced *S. jonesii* to the rank of subspecies under *S. rubra*, and recognized that its range was limited to the mountains of North and South Carolina.

Our interest in *Sarracenia rubra* began about 1953 when our own field studies, experiences, and observations seemed at odds with published information. Our observations and

studies over more than 20 years have led to the description of a new species, *S. alabamensis* Case & Case (1974), and to the conclusion that "*S. rubra*" represents a complex of taxa, all related, yet in some ways all subtly distinct. Before we present our data, we believe it will be helpful to consider the important taxonomic characters used by botanists in delineating species of *Sarracenia* and some of the problems involved.

SIGNIFICANT TAXONOMIC CHARACTERISTICS

The structural features most significant in distinguishing species of *Sarracenia* include leaf shape and size, types of leaves produced, size, shape, carriage and reflexion of the pitcher hood, presence or absence on the leaf of window-like areoles, details of leaf coloration, pubescence and substance.

Wherry apparently considered leaf size of prime importance in his early study of *Sarracenia jonesii*, but Bell (1949), commented as follows:

> "Size is of no value per se in species delimitation in this genus. Various ecological factors result in mature plants of many sizes within a given species. The extreme cases of this are shown in *S. minor* and *S. flava*, but less striking differences in size appear in all other species of *Sarracenia*. Size, therefore, is not a constant, and cannot be used as a basis for taxonomic differentiation."

We agree with Bell that ecological factors can produce great size variation among wild individuals of any species grown under diverse conditions; indeed, we feel that this ecologically induced variation is responsible for much of the past confusion in the *S. rubra* complex. We further agree that an occasional aberrant variant can occur within any given species, but we cannot agree that size in general terms is not constant; rather all of our studies indicate that there *are* definite, genetically controlled size trends for leaves and leaf parts in all species of *Sarracenia*. It is

not that size is of no value, but that ecological factors, acting upon developing leaves, affect the expression of leaf size and shape.

Within the parameters we have discussed in this paper, we agree completely with Bell (1949) when he says; "The over-all shape or form of the pitchered leaves is generally a constant morphological characteristic, and as such is the most useful single feature used by taxonomists in species delimitation within the genus *Sarracenia*."

While flower structure is most distinctive at the genus level, only petal color, petal shape, and to a lesser degree, flower size and scent have been used in species demarcation. Flower size is related not only to the species involved, but is also affected by the ecological situation, age, and vigor of the plant. The later flowers on a given plant tend to be reduced in size, sometimes significantly so over the earlier ones. There is enough overlap of size, petal shape, and scent between various species to render flowers of limited value for taxonomic differentiation.

The taxonomic usefulness of the leaf over the blossom in *Sarracenia* must be considered in light of the specialized function of the leaf. The hollow, tubular leaf is a pitfall, passive trap, complete with baiting fluids which paralyze or poison insects, as shown by recent studies (Sci. News **106**: 286. Nov. 2, 1974).

Plummer, *et al.* (1964) found that nutrition through insect trapping affects pitcher plant growth rates far more than had previously been appreciated. We found that we could bring two-inch plantlets of *Sarracenia flava, S. jonesii, S. alabamensis* subsp. *wherryi* × *S. minor,* and others to near flowering size in as few as 9 or 10 artificial feedings through the pitchers, about a month apart, while control seedlings scarcely grew at all.

In investigations related to his doctoral dissertation now in preparation, Thomas Gibson (personal communications, 1974-1975) has clearly established that when several species of sympatric sarracenias grow in the same bog, they

trap different species of native insects with little overlap between species.

It seems to us that there is sound evidence in *Sarracenia* of growth, competition, and survival factors which involve the trap-leaves. It is not surprising, then, that it is the leaves which have undergone the striking evolutionary changes and that floral structures have evolved less and are of less value in taxonomic studies. The principal works of the past, e.g., MacFarlane (1908), Harper (1918), Wherry (1929, 1935), Bell (1949), and McDaniel (1966, 1971), have made use of this leaf diversity; their works and identification keys make use of leaf structures coupled with petal color almost exclusively.

We have concluded that pitcher size of the largest leaves of the growing season, orifice width, hood length and width, scape height, and an index derived by dividing hood length by width yield the most reliable measurable data for pitcher comparison. When these data are related to color of mature, hardened leaves, venation patterns, hood carriage and reflexion, ratio between scape and leaf height, leaf substance and pubescence, overall flower size, petal shape, size and color, and geographic distribution, definite patterns emerge.

ECOLOGICAL RESPONSES DURING LEAF DEVELOPMENT

In a genus in which leaf characteristics assume great importance, it is essential to realize how ecological conditions affect leaf development. This is particularly so in *Sarracenia* where the unique, hollow pitcher complicates ecological response. Many factors directly affect leaf development; our observations and the meager published observations indicate that the response of leaves is essentially the same in all species.

MacFarlane (1908) comments that coolness, shade, and moisture all cooperate to affect reduced pitcher cavity, color intensity, and conformation of the laminar wing in all species, but he cites no definite experimentation. Bell

(1949), in considering *Sarracenia psittacina* discusses the influence of light upon its leaves:

> The leaves however, do show the effect of strong sunlight. Leaves of plants growing in shaded locations tend to be longer, greener, and have smaller hoods than those grown in the sun, which are often found with large hoods and almost solid red leaves.

Bell (1949, pp. 157, 158) also discusses the fact that red color of both leaf and flower in *Sarracenia purpurea* is influenced by intensity of sunlight. Wherry (1933), in discussing *S. purpurea* var. *heterophylla,* discusses the nature of the type specimen of *heterophylla,* and ascribes its elongated leaves to shading. Mandossian (1966) reports a laboratory experiment designed to test the effect of light intensity upon production of pitcher volume and laminar development in Michigan *S. purpurea.* She concluded that low light levels result in large, highly developed pitcher lamina and in "absorption" (reduction) of the pitcher. That this is true under both laboratory and field conditions, we can verify.

Unfortunately we have seen no thorough discussions of changes in leaf shape correlated with light intensity in the trumpet-leaved pitcher plants. But we have grown all species for over 20 years in our comparative cultures and out of doors, and have observed them in the field. All of the trumpet-leaved species respond in a similar manner. Given other requirements, growth is most vigorous and coloration most intensely developed in full sunlight. The pitchers, with relatively short, strong petioles, stand properly erect, with fully expanded pitcher and hood.

If light decreases from that of full sunlight intensity, changes occur in developing leaves. New leaves elongate significantly over previously formed leaves; petioles become weak; pitcher volume may at first increase slightly, but if shading persists, subsequent leaves become reduced in size and pitcher volume. The wing or lamina of the pitcher enlarges, especially in the mid-region of the pitcher.

The increased laminar wing warps the pitchered section into abnormal positions. In most species, the pitcher hood at first enlarges, but is ultimately sharply reduced. In heavily shaded specimens developing hoods may have difficulty in assuming a normal carriage.

In most species flowering is heaviest in fully sunlit plants. As light is reduced, flowering decreases. Heavily shaded plants seldom bloom at all, although members of the *Sarracenia rubra* complex, somewhat better adapted to brushy, shaded habitats than most species, retain the ability to flower sparingly even when shade-induced leaf deformation is considerable.

All sarracenias are hydrophytes. Other conditions being equal, the maximum growth potential of leaves is reached in the presence of an abundant water supply. If the water supply is reduced to a minimum that will maintain life for the pitcher plant at a time when it produces new leaves, changes in leaf form result, which are similar in all species. Pitcher volume becomes reduced, and the laminar wing increases markedly in proportion. In trumpet-leaf types such as *Sarracenia rubra,* new leaves become shorter, less inflated, often with hoods that barely open. Less anthocyanin pigment develops. In taxa which normally produce more than one set of pitchered leaves in one season, excessive dryness may result in failure to produce late season pitchers, or in the production of stunted ones.

The amount of peaty, organic material in the soil influences pitcher size in all *Sarracenia,* provided other requirements are met. Harper (1918) and Bell (1949) report unusually large leaves on *S. minor* growing on floating islands of rotting vegetation in Okefenokee Swamp, Georgia. Bell reports that leaves of these large forms reverted to a smaller, more typical form under his greenhouse conditions. Presumably the highly organic substrate plus abundant water influenced leaf size in the wild plants.

On the inner Coastal Plain near Lucknow, South Carolina, and in the Fall Line Sand Hills of Taylor County, Georgia, we collected large-leaved plants of *Sarracenia*

rubra. Shaded specimens, especially from the Georgia station, were very tall, reminiscent of *S. jonesii* Wherry. When removed to our greenhouses and grown in our prepared, uniform soil mix, all plants from these areas gradually reverted to a size typical of *S. rubra* from the more sandy, outer Coastal Plain soils.

Mandossian (1966), working with *Sarracenia purpurea* in Michigan, found that pitcher plants growing in a marly, mineral-type soil formed many crowns and numerous small pitchers; those in highly organic sphagnum bogs made fewer crowns and leaves, but were larger, more fully expanded. Reciprocal transplants readjusted morphologically in a very gradual manner; she found that plants needed at least two growing seasons to adjust leaf size and form from that typical of one habitat to that typical of another. She further cites the work of others to show that gradual adjustment of form over a long period is characteristic of many other plant species.

Ecological factors appear to influence pitcher plant leaf development strongly. One must use caution, therefore, in comparing similar leaved taxa unless they have developed under identical conditions for a considerable period of time.

SCOPE OF THE PRESENT STUDY

Our study of the *Sarracenia rubra* complex has been four-fold: 1) extensive field observations, 2) nearly 20 years of comparison of live material from all known "*S. rubra*" populations grown under standardized conditions in our greenhouses, 3) comparison since 1970 of plants of all populations grown out of doors in an artificially created wet sand bog, and 4) extensive leaf analysis utilizing not only material from our culture experiments, but also of specimens deposited in the herbarium collections historically important to this problem.

We performed minimal chromosomal studies, as the work of Bell (1949) and Hecht (1949) indicates that $n = 13$, $2n = 26$ in all species. The small size and size range of

the chromosomes in the entire genus (Bell, 1949) and in the "*S. rubra*" taxa in particular, and the difficulty of obtaining really good root tip observations in this genus, make karyological studies difficult. There is need for additional work. For chromatographic examination of the complex, we consulted specialists; their findings are generalized in this paper, and will be separately published by them.

FIELD POPULATION EXAMINED

We examined the major population centers of all species of *Sarracenia* so that we might understand the influence of hybridization and introgression upon the group. For all species which enjoy an extensive range, we visited a number of stations at various distant points within that range so as to obtain a broad sampling of study material. We have observed them at all seasons, winter, flowering, young leaf development, mature leaf, fruiting; in all we have examined thousands of living plants in the wild.

If one consults the distribution maps for *Sarracenia rubra* (sensu Bell, 1949, plate 12) or as treated by McDaniel (1966), one obtains the impression that "*S. rubra*" grows in suitable habitats more or less uniformly across the area of its range as shown on the maps. Our field studies do not confirm this. We found that there appeared to be five disjunct populations; four of these showed what we consider to be distinctive structural and behavioral differences.

If one plots the localities for existing herbarium specimens on a map, the distributions also fall into five disjunct groups which approximate the ranges of the populations as we determined them from our field studies of the past 20 years (see Fig. 1).

For our field observations and our comparative culture studies of the *Sarracenia rubra* complex we observed populations and obtained cultures from the following states and counties: Alabama: Autauga, Baldwin, Chilton, Elmore, Escambia, Mobile, Washington. Florida: Okaloosa, Santa

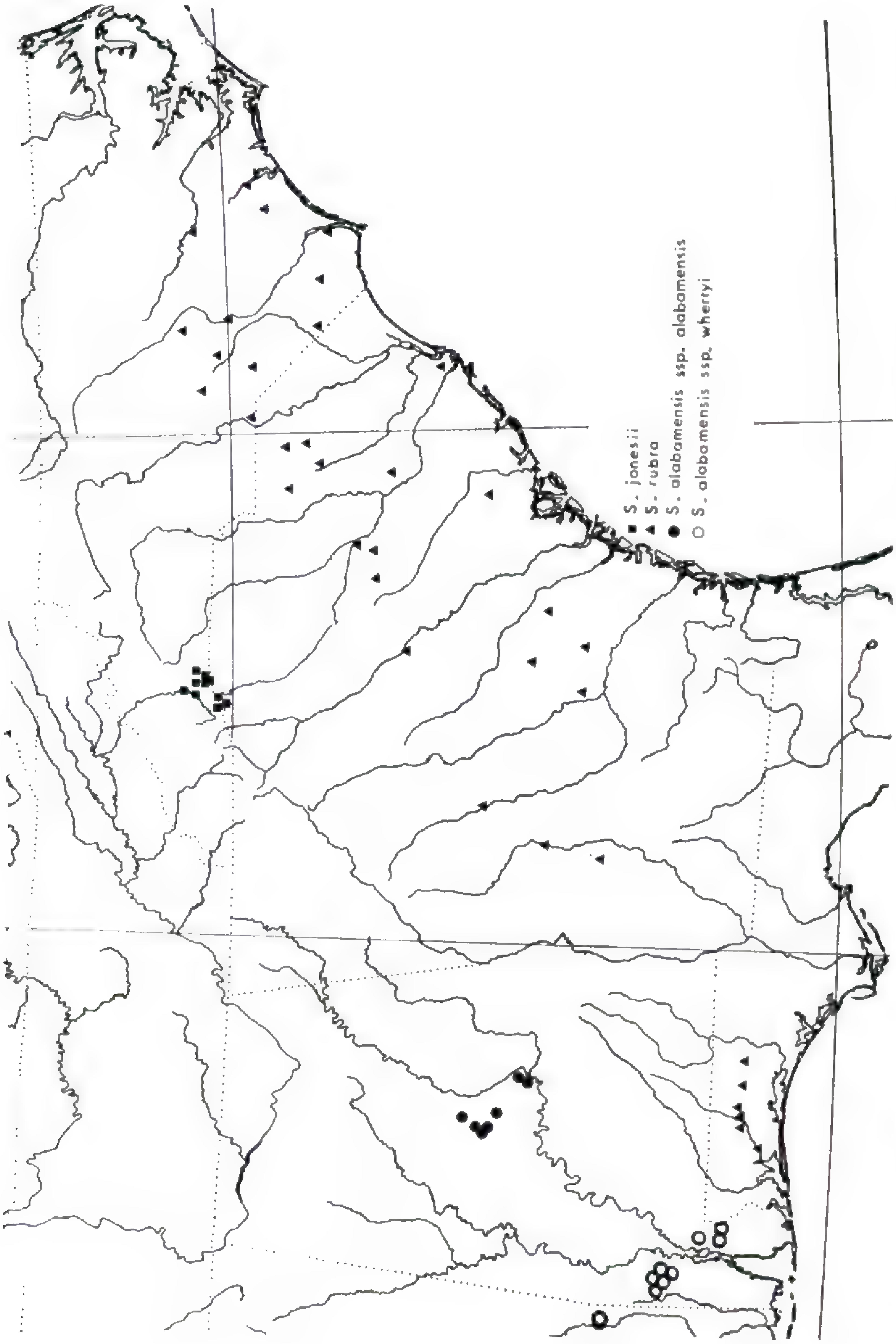

Fig. 1. Distribution of the *Sarracenia rubra* complex as determined by existing herbarium specimens which we have examined.

Rosa. Georgia: Taylor. North Carolina: Bladen, Brunswick, Columbus, Henderson, Transylvania, Buncombe. South Carolina: Georgetown, Horry, Kershaw, Lee, Pickens. Mississippi: Wayne.

Most of our observations on the various populations, based upon both field work and comparative culture, are summarized in Table 2, or in the taxonomic treatments in this paper.

MEASUREMENT PROBLEMS

In 1956, and again in 1972-75, we examined all the specimens of the *Sarracenia rubra* complex from the following herbaria: US, PH, PENN, NCU, NY, FSU, (1972-75 only) and Duke (1956 only).[1]

Many herbarium specimens are very difficult to compare with others. They are collected at nearly all seasons of the year; many are taken in flower and either lack leaves of the current season, or are taken with leaves not yet fully expanded. Pressing of the tubular leaf distorts the carriage and reflexion of the pitcher hood. Drying often destroys external pubescence, distorts substance, and destroys the subtleties of leaf color.

In addition, there was often the haunting suspicion that with the larger-leaved taxa, many herbarium specimens had been taken to fit the herbarium sheet rather than to represent the typical plant.

Our field observations, the published remarks of others, and the diversity of the herbarium specimens made us question whether the herbarium comparisons would be reliable. This concern proved to be unfounded (see fig. 2).

Another problem arose at this time. Past authors gave leaf measurements in broad general size ranges only. Since members of the *Sarracenia rubra* complex can produce

[1]We wish to thank the curators of the herbaria whose specimens we have studied. We are grateful to Dr. W. H. Wagner, Jr., University of Michigan, and to Dr. James Wells, Cranbrook Institute of Science, for their valuable counsel and for securing the specimen loans for us at various times in this study.

pitchers of many sizes on a given plant, a need to standardize comparisons and measurements seemed to us essential. We determined, therefore, to define our own leaf and hood measurements, thus hoping to eliminate the changes in hood carriage (and hence height) caused by pressing of specimens. We also determined to devise a standardized method of comparative culture which would eliminate as many of the ecological variables as possible.

MEASUREMENTS

MacFarlane (1908) pointed out that seedling leaves in all species of *Sarracenia* tend to resemble closely those of *S. minor* Walt., and do not show well the specific differences. We might not agree that all seedling or juvenile pitcher-leaves resemble *S. minor,* but our observations do show that specific differences show most clearly in the largest leaves of a growing season of vigorous flowering-size plants growing in full light. In order to standardize comparison of the taxa in our comparative cultures, we measured only the two largest leaves produced by a flowering rhizome terminus of a given clone that season. For herbarium material, the only standardization possible was to measure the one or two (if present) largest complete leaves on the specimen.

MEASUREMENT TECHNIQUE

We measured pitcher leaf length from the point of attachment of the amplexicaul base to the rim of the pitcher orifice. Such leaf measurements do not include the hood. Hood length refers here to the distance from the narrowest part of the hood constriction (or neck) to the tip of the hood, while hood width refers to the distance across it at its widest point.

To facilitate measurement comparisons of the tubular pitcher between fresh and herbarium materials, we give width figures for flattened pitchers rather than diameters for expanded ones.

Scape height measurements run from point of basal attachment to the attachment of the sepals. Petal length and width represent the structure's greatest dimensions.

There are distinctive differences in pitcher taper and expansion in the *Sarracenia rubra* complex. These are subtle, and can be affected by ecological factors present as the leaf develops. The same is true for the carriage of the hood over the pitcher orifice and its manner of reflexion. Color patterns vary not only among the populations, but in the same taxon or clone in relation to leaf age, health, and the amount of sunlight the leaf received. We found no truly satisfactory method to measure these characteristics statistically. Yet there are characteristics distinctive to each population. These are best described or illustrated in the appropriate sections of this paper.

COMPARATIVE CULTURE METHODS

We brought together, in our greenhouses at Saginaw, Michigan, plants of each of the taxa collected by us from the wild. We chose plants at random, where possible, but we did make an effort not to select plants of obviously hybrid origin. We grew our plants in an east-west oriented Everlite greenhouse. We placed the plants to be compared on the benches in north-south rows so that all plants would receive approximately equal lighting during the day and none would seriously shade the others. Tops of the plastic flowerpots stood above the base of the greenhouse glass; thus the plants received maximum available light. No shading was used on the glass of the greenhouse, and plants received full sunlight throughout the day, excepting in very late summer, when the plants were shaded from direct sun's rays after 3:00 P.M. by a nearby building, but there was always open sky directly overhead. Light was uniform and strong; during July and August, 1974, we checked the intensity of the light daily between 11:00 A.M. and 2:00 P.M. with a Gossen, Luna-Pro incident light

meter. We found the plants received 4,000 to 8,000 foot-candles of light, depending upon the degree of cloudiness.

Plants received the normal photoperiod for this latitude. In winter, we gave them a dormant period at ± 0°C for two months. Growth commenced in late February, and the plants in the greenhouse here bloomed at the same time as that usual for wild plants in the Gulf Coastal states, i.e., early April.

During the summer months, open windows and doors admitted many insects which the pitcher plants captured in great numbers.

To provide a uniform growing medium to all plants, we compounded soil using six parts washed silica sand (obtainable at builder's supply stores) with four parts commercially packaged Canadian (sphagnum) peat, thoroughly mixed together. Rhizomes were planted at the surface of the mix.

To assure uniform moisture to all plants, we made trays approximately two inches deep and lined these with 10 mil polyethylene sheeting to make a shallow tank. Pots stood in this tank with the soil surface approximately 5 inches above the water level; all pots received the same water supply. The water used came from a surface well which drained from acid sands; its pH averages 6-6.5, and the native vegetation in the damp places near the water source included such acid-soil and bog plants as *Vaccinium* sp., *Sphagnum* sp., *Osmunda regalis, Liparis* sp., and *Spiranthes* sp.

Specimens used in our comparative studies grew under these conditions for at least three years, most of them for more than 10 years.

In all cases, their growth was in every way typical for all known species of *Sarracenia,* and our plants produced vegetative parts which were within the size ranges of the existing herbarium material from the same areas as our study plants and within the size ranges of plants we have observed in the field.

FINDINGS

Figure 2 shows leaf size ranges from 6 distinct population areas representing 4 taxa. Figures 3 and 4 present data on pitcher size vs. hood length/width ratios for the 6 populations. Analysis of measurable data for several useful taxonomic characters is compiled in Table 1.

To determine if the population differences represented chance variation or whether the variation was significant, we performed an analysis of variance on the five leaf and scape measurements (see Table 1), and found in each case that the degree of significance was well above the 0.5% level, indicating that the chance that these specimens belonged to a single population was extremely small. The specimens of the Taylor Co., Georgia, area and those of the disjunct western Florida area, while differing from the plants of the Carolina-Georgia Coastal Plain area in leaf size and shape, differed from them to a much lesser degree than those plants differed from other populations. When this information is coupled with other structural similarities shared by these populations and not found in the others, and with what we believe has been the geological history of the group, we considered that these particular populations, even though disjunct, represent one specific entity.

In all measurements, our data on the 6 populations show significant grouping into 4 structurally distinct taxa, both for comparative culture and for wild specimens. We had not expected that the wild specimens would show the natural groupings so clearly, in view of the great influence ecological conditions exert over pitcher size and conformation in *Sarracenia.* The smaller sizes of the comparative culture material over wild (fig. 2) reflect the response of the material to uniform conditions in which shade effects (etiolation), moisture, and soil differences were eliminated. Our comparative culture material we consider to represent healthy, normal plants; many of our study clones have thrived in our culture for 10-20 years, all bloom profusely,

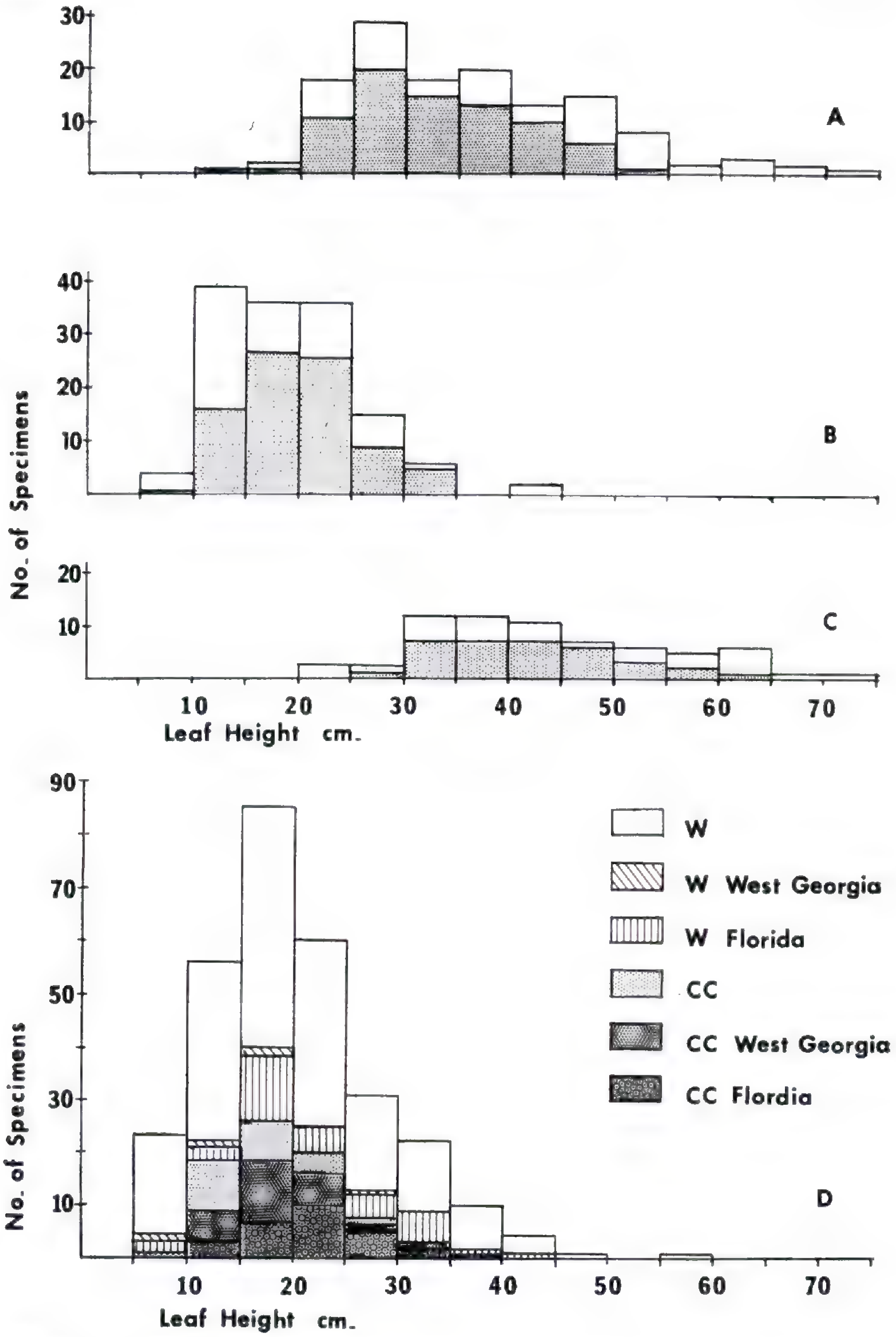

Fig. 2. Leaf height and number of specimens examined for 4 taxa comprising the *Sarracenia rubra* complex. W = wild (herbarium specimens), CC = our comparative culture material. The taxa are: A, *S. alabamensis* subsp. *alabamensis;* B, *S. alabamensis* subsp. *wherryi;* C, *S. jonesii;* D, *S. rubra.*

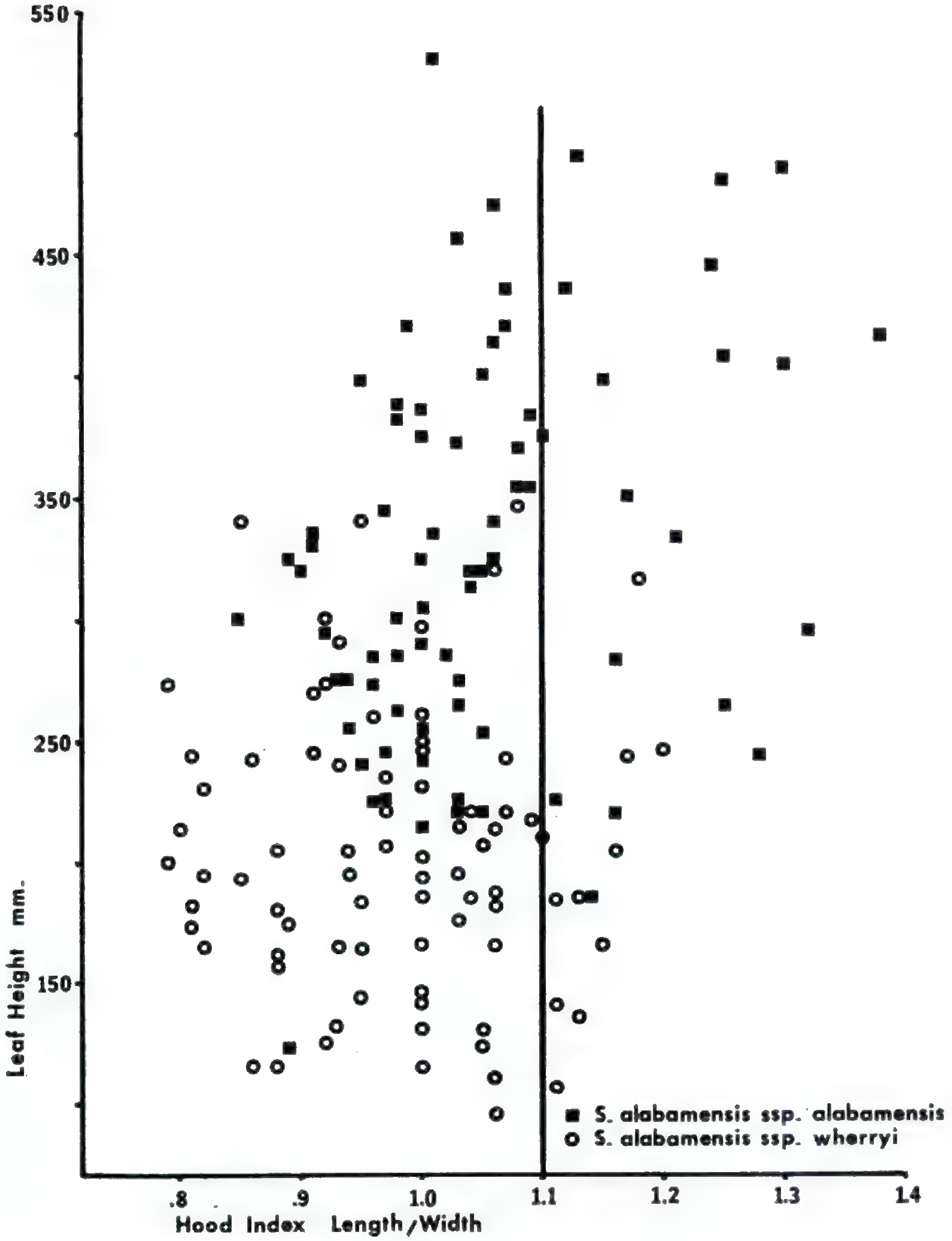

Fig. 3. Leaf height and hood length/width index comparison for *Sarracenia alabamensis* subsp. *alabamensis* and *S. alabamensis* subsp. *wherryi*.

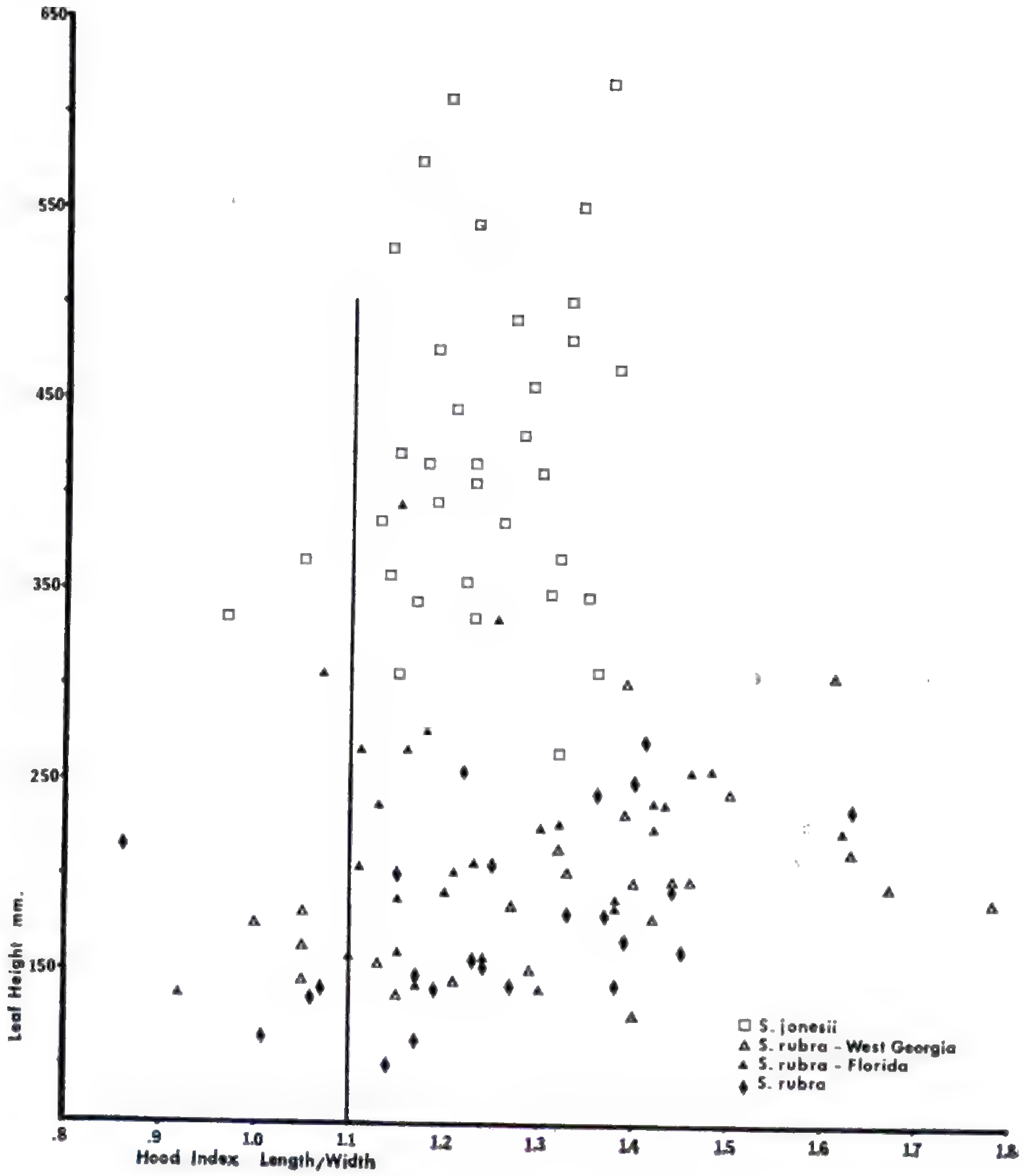

Fig. 4. Leaf height and hood length/width index comparison for *Sarracenia jonesii* and *S. rubra*. The *S. rubra* from 3 extremities of its range are plotted separately: diamond symbol = *S. rubra* of the Carolinas, both inner and outer Coastal Plain stations, open triangles = *S. rubra* from the inner Coastal Plain, Fall Line hills of Taylor Co., Ga., (a possible disjunct colony), and solid triangles = *S. rubra* from the disjunct, Western Florida population.

Table 1. Analysis of measurable data on the two largest leaves available for leaf height, leaf structures, and scape height for both our comparative culture specimens and herbarium specimens (in mm). W = wild or herbarium specimens, CC = comparative culture material. M = mean, s = standard deviation, r = range, and n = number in the sample. F*, in the F distribution, a number larger than 2.7 would indicate a significance beyond the 5% level; a number greater than 4.5 would indicate a significance beyond the .5% (F .995) level.

		Leaf Height		Orifice Width		Hood Length		Hood Width		Hood Index (Length/Width)		Scape Height	
		W	CC	W	CC	W	CC	W	CC	W	CC	W	CC
S. alabamensis ssp. *alabamensis*	M	408.6	330.5	26.9	35.8	39.7	50.8	33.4	48.5	1.18	1.05	398.0	443.2
	s	140.5	82.7	10.2	8.2	14.9	12.1	11.0	11.2	0.17	0.11	83.5	62.8
	r	185-717	122-530	7-48	17-67	7-71	25-90	8-50	22-88	0.81-1.58	0.85-1.38	270-571	320-572
	n	52	78	51	78	40	76	40	76	40	76	35	14
S. alabamensis ssp. *wherryi*	M	183.2	201.7	14.6	19.8	22.0	27.2	21.1	28.0	1.05	0.98	264.0	302.3
	s	79.3	56.7	4.6	6.1	9.3	7.8	8.2	8.6	0.16	0.10	73.4	59.0
	r	80-450	95-347	7-28	9-42	8-45	17-46	8-40	13-54	0.67-1.7	0.79-1.2	137-385	227-455
	n	55	84	54	86	44	85	44	85	44	85	35	14
S. jonesii	M	445.3	422.8	28.4	23.1	45.2	42.3	36.7	34.4	1.24	1.23	442.6	498.7
	s	142.7	87.1	8.0	5.2	10.5	7.8	7.4	6.5	0.21	0.12	111.0	104.2
	r	210-730	262-615	10-42	15-42	24-65	26-57	24-54	20-50	0.91-1.67	0.97-1.38	325-690	351-696
	n	33	34	30	34	20	34	20	34	20	34	23	28
S. rubra	M	208.3	196.4	12.0	15.1	23.3	26.4	16.2	20.6	1.46	1.29	379.7	459.2
	s	89.1	54.3	4.8	5.7	7.1	8.3	5.9	6.1	0.41	0.19	90.7	109.2
	r	57-570	100-395	5-28	7-40	7-45	14-53	7-39	9-38	0.8-4.3	0.86-1.78	170-630	293-661
	n	216	79	189	79	90	78	90	78	90	78	117	44
	F	99.1*	131.8*	116.4*	141.5*	48.3*	120.4*	63.3*	144.1*	19.9*	80.4*	22.3*	14.7*

TABLE 2

Characteristic	*S. jonesii*	*S. rubra*	*S. alabamensis* subsp. *alabamensis*	*S. alabamensis* subsp. *wherryi*
Pitcher types	all alike	all alike	spring pitchers small, sigmoidly recurved wing broad, volume small, green-bronze. Summer and fall pitchers large and voluminous, bright yellow-green.	all alike
LARGEST LEAVES:				
Height & width	tall and thin	short and thin	tall and wide	short and wide
Petiole	long; ¼ to ⅓ length of pitcher	very short; less than ¼ length of pitcher	medium; about ¼ length of pitcher	short; less than ¼ length of pitcher
Pitcher chamber	expanding rapidly in upper ¼. Somewhat bulged on abaxial surface below hood neck	very gradualy tapered from base to orifice	expands uniformly but rapidly widening to wide orifice	expands from leaf base gradually to orifice, often widest just below orifice
Upper pitcher tissue substance	firm, thick, waxy; glabrous to puberulent	very firm, thick, waxy; glabrous to puberulent	thin, soft; densely fine pubescent	soft; very densely fine-pubescent

Orifice rim	scarcely or not flared, rim tightly rolled, narrow	not flared, tightly rolled, narrow	strongly flared, loosely or irregularly rolled	weakly flared or not flared, moderately tightly rolled
Rim color	green to dark maroon	dark green to maroon	iridescent-light yellow-green	yellow-green, rarely maroon flushed (hybrids?)
Rim carriage	horizontal or gradually sloping downward from hood to wing	horizontal or barely deflexed at orifice wing juncture. Most often raised slightly at juncture	tapering gradually downward to wing juncture, but with a large spout-like indentation at juncture	variable, but with a noticeable downward indentation at region of orifice wing juncture
Markings: Color of mature sunlit leaves	green, upper leaf veins and sometimes other tissue suffused with dark maroon-purple, particularly on inside of hood neck	dull green, young leaves suffused with reddish-brown which is replaced in most mature leaves by a dark maroon overlay; veins dark maroon	yellow-green overflushed faint red until mature, becoming light green or golden-green in upper portion	dull light green, bronze-red flushed
	veins colored on both outer and inner surface of pitcher	veins colored on outside and inside of pitcher	veins colored maroon on inside pitcher surface only	veins mostly colored on inner pitcher surface, color may show through to outside
			faint whitish-green areoles irregularly present	

TABLE 2 — Continued

Characteristic	*S. jonesii*	*S. rubra*	*S. alabamensis* subsp. *alabamensis*	*S. alabamensis* subsp. *wherryi*
Hoods	longer than wide; cordate, green or maroon flushed, veins colored on both surfaces to hood margin; slightly reflexed	generally longer than wide; ovate, veins of both surfaces colored to margins; not reflexed; veins of neck very strongly colored forming a distinct dark patch	often wider than long; upper surface convex-puckered; clear golden-green, outer veins green or faintly colored in proximal ½ only; strongly reflexed	usually as wide or wider than long; green-bronze flushed; main veins of inner surface colored maroon, outer surface often all green, rarely colored; slightly to moderately reflexed
	faintly undulate	not undulate	broadly undulate	convex, weakly undulate to not undulate
Phyllodia	none	none	very occasional, flat and recurved; produced in early summer	none
Rhizome branching pattern	moderate, small clumps unless disturbed	moderate, forms small clumps	strongly branching, forms large, dense clumps	sparse to small clump former
Relative bloom time in comparative culture	late, last to bloom, 7-9 days after *S. rubra*	late-mid season, starts as *S. alabamensis* finishes	starts 10 days after subsp. *wherryi*, early mid-season	very early, first to bloom

Petal carriage	flat, pendant, not spreading	flat, pendant, lateral margins of distal lobe frequently inrolled	spreading-pendant, flat	flat, pendant, distal lobe becoming reflexed (from *S. alata?*)
Sepal carriage	moderately reflexed	very strongly reflexed	strongly reflexed	weakly reflexed to flat and falcate-curved
Winter photoperiod response (not frozen)	nearly evergreen	essentially evergreen	partial dieback, leaf bases evergreen	nearly total dieback

Table 2. Comparison of the 4 taxa of the *Sarracenia rubra* complex for some useful distinguishing features not easily measured.

and the size ranges of our specimens are within the size ranges of wild specimens from the same localities. Our largest leaves of *S. alabamensis* subsp. *alabamensis* for 1974 matched in size, color and conformation the largest leaves of wild plants from Chilton Co., Alabama, collected by Thomas Gibson and brought to Saginaw, Mi., for comparison.

Besides the size differences, each population differs in structural features which are not susceptible to precise measurement but which are nevertheless distinctive. Table 2 presents a comparison between the taxa for some of these and other features as do figures 5 and 6.

Fig. 5. A, *Sarracenia jonesii*, Transylvania Co., N. C. B, *S. rubra*, inner Coastal Plain plant from Lucknow, S. C., and C, *S. rubra*, from outer Coastal Plain near Georgetown, S. C. These 3 clones were grown 6 inches apart in an artificial bog garden outdoors at Saginaw, Michigan for 3 growing seasons. Plant B, when collected, had pitchers nearly as tall as those of *S. jonesii* and would have been considered an "intergrade" by some authors.

Fig. 6. Leaves of the 4 taxa comprising the *Sarracenia rubra* complex, selected because they approximate in size the mean for material grown under our comparative culture method. In pairs, left to right, *S. jonesii*, *S. rubra*, *S. alabamensis* subsp. *alabamensis*, and *S. alabamensis* subsp. *wherryi*.

It is particularly important to realize that the significant population groupings based on structural differences also represent populations geographically segregated from each other.

CHEMICAL INVESTIGATIONS

To see if comparative phytochemistry might show some significant trends within the *Sarracenia rubra* complex, we asked Dr. John Romeo, Chemical Plant Taxonomist, Oakland University, Rochester, Michigan, to examine our com-

parative culture plants. The work was carried out on all species of *Sarracenia* from our comparative cultures during June and July, 1975, at Oakland University, and at the University of Texas, Austin, Texas. Chemical analysis for amino acids and alkaloids, using chromatography and electrophoresis techniques, indicates only common protein amino acids present, with no significant differences between species. No alkaloids were detected by Romeo (personal communication, 1975).

Professors Romeo and Mabry also examined flavonoid compounds of all species of *Sarracenia* by paper chromatography. Study on these compounds is being continued by Romeo, Mabry, et al. The results of their chromatography allow no sweeping conclusions. The number of flavonoids present is too few, and the overlap of compounds between taxa too great to be of conclusive value in determination of speciation in the *S. rubra* complex. However, a pattern did emerge which we feel supports our conclusions drawn from structural and geographic data.

Plants of *Sarracenia rubra* from the inner Coastal Plain near Lucknow, South Carolina, and the outer Coastal Plain near Supply and Shallotte, North Carolina, and Georgetown, South Carolina, showed significant chemical differences from others of the complex in having two compounds present in large amounts which were not present in others of the complex, excepting in specimens of *S. jonesii* from Pickens Co., South Carolina, and Buncombe Co., North Carolina (but not all *S. jonesii* tested).

Four of five samples from Florida share a compound with three of four *Sarracenia jonesii* and one of the Carolina-Georgia Coastal Plain population. None of the other members of the *S. rubra* complex contains this compound, but it also occurs in *S. minor* and in two populations of *S. purpurea* tested.

Plants of the Flint River drainage in Taylor Co., Georgia, shared weak amounts of a compound in common with plants from Florida but differed from the Carolina Coastal Plain *Sarracenia rubra* in some compounds.

A compound present in most clones of *Sarracenia alabamensis* subsp. *alabamensis* occurs also in plants from Perdido, Alabama, but not elsewhere in the *S. rubra* complex. Plants of what we regard as belonging to the same basic population as those from Perdido, from near Fruitdale and Citronelle, Alabama, lack this compound. However, the Fruitdale-Citronelle area is one of particularly high incidence of hybridization among several pitcher plant species. McDaniel (1966) states "chemical introgression may occur in populations where extensive hybridization occurs." Considerable variation in trace amounts of four compounds in our material from this region suggests such introgression has indeed occurred.

The several pairs of populations which share flavonoid compounds between them which are not found elsewhere in the *Sarracenia rubra* complex suggest to us a relationship between them which agrees strongly with our geologic-geographic conclusions, and we will discuss it in that section of this paper.

TAXONOMIC TREATMENT

Field observation, structural differences, size differences, pitcher dimorphism in one population, and the isolation of clusters of subtle but distinctive traits in disjunct populations, clearly indicate that what has been called *Sarracenia rubra* consists of four or five discrete taxa depending upon where one draws the structural limits.

All of the populations appear superficially similar. It would be easy to call them all one species and to designate the individual populations as subspecies, but we do not feel that such a treatment would reflect a true evolutionary picture. There are other considerations. No two taxa are known to be truly sympatric and good evidence of intergradation between members of the different taxa does not exist. Plants such as those cited by Bell (1949) or McDaniel (1966) as intermediates between *Sarracenia rubra*

and *S. jonesii* can be shown to be ecological forms, or explained as complex hybrids (see discussion of *S. rubra*).

In our comparative cultures, in the greenhouse and out of doors, each taxon flowers at a slightly different time at a given locality; therefore, if they did grow together, interbreeding would not normally occur. Each population differs from the others in leaf size, color, texture, shape, hood size and shape, and in flower size and petal shape. One population differs substantially in producing dimorphic pitchers.

Hybrids formed between members of one population of the complex and a common other parent (*Sarracenia purpurea* subsp. *venosa*) differ in leaf size, proportion and texture from hybrids between members of other populations of the complex and the same common parent (fig. 7).

After careful consideration of our statistical data (Table 1) and of our field observations, and especially after our more than 20 years of observation of these plants growing under standardized conditions, we believe that the following taxonomic treatment best reflects the situation found in nature.

The following key relies primarily upon the types of leaves produced, and the characteristics of the fully matured, largest leaves of the growing season which have developed in bright sunlight. Because of the effects of ecological conditions pointed out in this paper, several specimens from a population will usually key better than a single specimen. Unless an herbarium specimen has been specially prepared and dried rapidly under heat, details of color, texture, and pubescence become obscured, rendering the specimen very difficult to use. We recommend, where possible, use of fresh leaves.

While we do not consider geographic location an ideal key character, the members of the *Sarracenia rubra* complex may be "keyed out" geographically, as each of the taxa is disjunct from the others of the complex. We have, therefore, included this information in the key.

Fig. 7. Leaf samples of hybrids between *Sarracenia purpurea* subsp. *venosa* and 3 members of the *S. rubra* complex: left to right, *S. jonesii* × *S. purpurea*, Transylvania Co., N. C.; two specimens, two clones, *S. rubra* × *S. purpurea*, Brunswick Co., N. C.; and *S. alabamensis* subsp. *wherryi* × *S. purpurea*, hand pollinated hybrid produced by us, both parents from Washington Co., Alabama. All leaves from flowering-sized plants in comparative culture, although we have seen and had leaves on the *S. jonesii* hybrid up to 3 times larger than the specimen pictured.

A KEY TO THE RED-FLOWERED, TRUMPET-LEAVED SPECIES OF SARRACENIA

A. Upper portion of pitcher-tube and hood strongly white-areolate, the areoles greatly exceeding in area the thicker, photosynthetic tissue between. Hood margins strongly undulate. Erect, gladiate laminar phyllodia usually present. .... *S. leucophylla.*

AA. Upper portion of pitcher-tube and hood without areoles, or if areolate, obscurely and irregularly so, with pale yellowish-green or whitish-green areoles. Hood margins without undulation, or with a few irregular, broad undulations. Phyllodia, if present, few, obscure, recurved-decumbent. .... B.

B. Pitcher tissue below orifice thick, almost waxy, the outer surface glabrous to puberulent (under magnification). Orifice rim tightly rolled, its juncture with the pitcher wing usually not indented, if indented, neither strongly so nor does indentation form a conspicuous, somewhat everted spout which extends forward over the pitcher wing. Orifice rim, major veins of both inner and outer pitcher tube, main and branch-veins of inner neck of hood strongly colored red-purple, the coloring of the hood veins extending to hood margins on both surfaces. Hood not reflexed or only slightly reflexed above neck. .... C.

C. Pitchers 21-73 cm tall (average 45 cm), long petiolate, the solid petiolar portion up to 1/3 the length of the leaf; abaxial portion of the petiole flattened in cross section, resembling an inverted T. Pitcher chamber diameter narrow, expanding sharply in upper ¼ of tube. Orifice diameter 1-4 cm wide. Neck of hood long, hood ascending, held high over the orifice, cordate, its margins weakly to moder-

ately reflexed, 2.4-6.5 cm long, 2.4-5.4 cm wide. Flower scapes about equalling pitcher height. Plant of the Blue Ridge Mountains of western Carolinas. .... *S. jonesii.*

CC. Pitchers 5.7-57 cm tall (average 21 cm), short petiolate, the solid petiolar portion less than ¼ the length of the pitcher; abaxial portion of the petiole rounded in cross section. Pitcher chamber diameter relatively narrow throughout, evenly and gradually tapered upwards, orifice 0.5-2.8 cm wide. Neck of hood short, hood usually carried close over orifice in a plane at nearly right angles to the long axis of the pitcher (less so in Florida population), its margins scarcely or not at all reflexed, 0.7-4.5 cm long, 0.7-3.9 cm wide, ovate. Flower scapes 1.5-2 times height of leaves. Plant of the Carolina-Georgia Coastal Plain and Fall Line Hills, with a disjunct area in western Florida. .... *S. rubra.*

BB. Pitcher tissue below orifice thin, densely fine-pubescent. Orifice rim loosely rolled, orifice at rim often slightly flared-everted, its juncture with the pitcher wing strongly indented and everted, forming a spout which extends slightly forward over the wing. Orifice conspicuously yellow-green. Upper pitcher green to golden-green, occasionally copper-red flushed. Major veins of upper pitcher-tube red-purple on inside of the tube only (although color may show through leaf tissue, especially in dried material). Veins of outside of hood of the same color as the tissue between veins. Veins of inner neck and hood, if colored, colored on main veins only, the colored portion not extending into puberulent distal portion of hood. .... D.

D. Spring and late summer pitchers unlike in size, volume, and often shape; the spring leaves shorter, narrower, usually sigmoidly curved; flushed red-bronze when young. Summer pitchers not decidedly recurved, much exceeding spring leaves in height and volume, light clear green to golden-green, 18-71 cm tall (average 40 cm); orifice 1.7-6.7 cm in diameter. Area below pitcher rim with a few to many scattered obscure, light greenish-yellow to whitish areole-like mottlings on outer surface. Hoods very large, neck broad, hood 2.5-9 cm long, 2.2-8.8 cm wide, moderately to strongly reflexed, its margins with a few broad, irregular undulations. Mature hood tissue between veins conspicuously convex-puckered, yellow-green on outer surface. Veins of the hood uncolored above and in distal half below. Flower scapes 27-57 cm tall, exceeding the spring leaves and about equalling the summer ones. Plant of the Fall Line Hills of central Alabama north of the Black Belt soils. .... *S. alabamensis* subsp. *alabamensis*.

DD. Spring and late summer pitchers essentially alike in size, volume and shape, dull green, flushed strawberry-bronze upwards, without areoles, 8-45 cm tall (average 18 cm); orifice 0.7-4.2 cm wide, tube often wider below orifice. Hood 0.8-4.5 cm long, 0.8-4 cm wide, overarching orifice to suberect, as wide or wider than long, veins of either surface varying from no red coloring to red-purple on major veins only, color extending to distal portion of hood only in some clones. Flower scapes 14-38.5 cm tall, equalling or slightly exceeding tallest leaves. Plant of southwestern Alabama and eastern Mississippi on both sides of the area of the confluence of the Tombigbee and Alabama Rivers. .... *S. alabamensis* subsp. *wherryi*.

1. *Sarracenia rubra* Walter, Fl. Carol. 152. 1788.[2]

Leaves semi-evergreen, dying back 1/3-2/3 only if severely frosted. Largest seasonal leaves of flowering plants relatively narrow throughout, gradually tapered from base to orifice, 5.7-57 cm tall, 0.5 to 2.8 cm wide; lateral wing relatively wide and prominent, often widest at or slightly below the middle, green becoming suffused with maroon tones in older, fully sunlit leaves, Florida forms often maturing to dark solid maroon colors. Leaf texture waxy, firm, rim of mature pitcher essentially horizontal (i.e. at right angles to main axis of pitcher); rolled rim not especially prominent, becoming dark maroon or dull green, the point of juncture of rim with lateral wing raised slightly or on the same level as the rest of the pitcher rim, or barely indented. Hoods as measured by us longer than broad, 0.7 to 4.5 cm long, 0.7 to 3.9 cm wide; ratio of length/width .98 to 4.3 in East Coast population, 0.8 to 1.5 in Florida population; hood suberect, carried close over the orifice; neck of hood not particularly contracted at base, the major veins and cross-veins of both outer and inner pitcher and hood surfaces becoming dark maroon-red with color spreading in Florida and west Georgia forms to mesophyll between vein reticulations, usually remaining green except on veins in Carolina material; veins of inside of hood colored maroon throughout entire distal, hirtellous portion (see fig. 6). Flower scapes erect, usually 2-3 times taller than tallest leaves, 17.0 to 66 cm tall in Atlantic coastal material, 26.5 to 48 cm tall in Florida population. Sepals 1.5 to 2.7 cm long, 2.0 to 2.6 cm wide, slightly narrowed or contracted beyond the middle in many individuals, maroon or greenish-maroon mottled on outer surface, the inner surface mostly green; lateral margins becoming strongly replicate over mid-line until they touch; calyx also recurving strongly away from the ovary after anthesis. Petals maroon, often on both surfaces, or with greenish suffusion on inner surface, panduriform, the basal cuneate

[2]For synonomy of *S. rubra* see Bell (1949).

portion relatively small, the distal lobe obovate, tending to be very strongly so; petals 2.5 to 4 cm long, the distal lobes 1.3-2.5 cm wide. Style disk 2 to 3.5 cm in diameter, 2-cleft, the margins of the cleft often overlapped. Mature capsules 0.5 to 1.5 cm in diameter, densely tuberculate.

Type locality: South Carolina, presumably on the Santee River.

Distribution: Very local, rapidly becoming rare in some districts, in bogs, swamps, and the Coastal Plain savannahs, or on springy hillsides near the Fall Line of Georgia, ranging from the Cape Fear River system in North Carolina locally southward to the Altamaha River system of the Atlantic Coastal Plain, southward ranging farther inland toward the inner Coastal Plain and Fall Line Sand Hills. Very local on the Flint River watershed system in western Georgia. A disjunct population more variable in leaf size and shape occurs in Walton, Santa Rosa and Okaloosa Counties in western Florida.

Representative Specimens: **Florida:** OKALOOSA CO., 3 mi W of Crestview, *E. T. Wherry* (PENN); Milligan, *J. M. MacFarlane* (PENN); 4 mi E of Crestview, *A. N. Leeds* (PH); swamp, Shoal River, *H. H. Hume* (DUKE); Adams Church near Crestview, *S. T. McDaniel* (FSU); margin of pond 1 mi E of Crestview, *R. K. Godfrey* (FSU); SANTA ROSA CO., 5.2 mi SE of Fla 87, vicinity of Yellow River N of Holley, *H. E. Ahles* (NCU); WALTON CO., ca 16 mi NE of Niceville, *J. Beckner, C. Chapman & R. R. Smith* (NCU); DeFuniak Springs, *A. H. Curtis* (US); margin of swamp, *A. H. Curtis* (NY). **Georgia:** BIBB CO., near Lakeside, *T. Darling, Jr.* (PENN); BULLOCK CO., Statesboro, *H. W. Trudell* (PH); COLUMBIA CO., 12 mi N of Augusta, *J. M. MacFarlane & W. Davis* (PENN); EMANUEL CO., bog in pine barrens near Graymont, *R. M. Harper* (NY); MACON CO., Toadever Creek, 8 mi SE of Reynolds, *J. H. Pyron & R. McVaugh* (PH); MONTGOMERY CO., swamp in sand hills west of Erick, *R .M. Harper* (US); SUMTER CO., sandy bog SE of Americus, *R. M. Harper* (US); sandy bogs, *R. M. Harper* (NY); TATTNALL CO., 1 mi S of Ohoopee, *R. M. Harper* (US). **North Carolina:** BRUNSWICK CO., Wilmington, *E. T. Wherry* (US); COLUMBUS CO., 4 mi S of Cerro Gordo, *C. R. Bell* (NCU); savannah near Brunswick, *A. E. Radford* (NCU); CUMBERLAND CO., vicinity of Fayetteville, *R. A. Clark* (DUKE); HARNETT CO., open bog, Overhills, *H. Laing* (NCU); HOKE CO., 4 mi SW of Montrose on Mountain Creek, *H. E. Ahles* (NCU); MONTGOMERY CO., 5½

mi SE of Candor, *A. E. Radford* (NCU); ONSLOW CO., Jacksonville, *H. J. Oosting* (DUKE); 2½ mi E of Onslow-Pender Co. line on NC 35, *H. E. Ahles* (NCU); RICHMOND CO., Hamlet, *W. W. Ashe* (NCU); SCOTLAND CO., 2.9 mi N of Silver Hill, *H. E. Ahles & R. S. Leisner* (NCU); 10 mi N of Laurinburg on Rt. 70, *C. R. Bell* (NCU); WAYNE CO., 5.8 mi E of Mt. Olive, *C. J. Burk* (NCU). **South Carolina:** CHESTERFIELD CO., between Cheraw and Sugar Loaf Mountain, *L. F. Ward* (US); CLARENDON CO., ½ mi S of Manning, *W. Stone* (PENN); COLLETON CO., *C. R. Bell* (NY); DARLINGTON CO., Hartsville, *J. B. Norton* (US); Seaboard R.R., W of Hartsville, *J. B. Norton* (NCU); GEORGETOWN CO., 5½ mi S of Georgetown, *R. K. Godfrey & Tyron* (NY); LANCASTER CO., near Kershaw, *H. D. House* (US); LEE CO., 2.7 mi N of Lucknow, *A. E. Radford* (NCU); LEXINGTON CO., 4 mi NW of Edmund, *A. E. Radford* (NCU); 5 mi S of Columbia, *Godfrey & Tyron* (US); thicket just N of Gaston, *E. T. Wherry* (PENN).

We restrict the epithet *rubra* to the plants from the Coastal Plain and Sand Hill regions of Georgia, North and South Carolina, and to the local disjunct population in Walton, Santa Rosa and Okaloosa Counties in western Florida. Plants of the Carolinas are the most uniform, tending to produce green, maroon-veined pitchers of small size and volume, a closely arching hood which is longer than broad, and without reflexed margins. The pitcher chamber tapers only slightly, the pitcher is nearly as wide below the middle as above it, and the point of juncture of rim and pitcher wing is often slightly raised. The scapes of the delicately small flowers usually exceed the leaves by 2-4 times.

Our concept of this species differs from that of MacFarlane, Bell, and McDaniel. MacFarlane did not recognize races or taxa within the *Sarracenia rubra* complex. Wherry, rightly as we believe, considered the Carolina mountain plants a distinct although allied species, *S. jonesii*. Unfortunately, the many shade ecads, introgressed hybrids of western Florida and Alabama, and plants of *S. alabamensis* from central Alabama confused him and he ascribed to *S. jonesii* a range in Alabama, Florida, and Mississippi which actually did not exist and which he later corrected (Wherry, 1972).

Most of the controversy over the *Sarracenia rubra* complex stems from the early misunderstanding of the nature and range of *S. jonesii.* Bell (1949), believing that the only reliable character which distinguished *S. jonesii* from *S. rubra* was the distinctive pitcher taper, and that this pitcher form occurred throughout the range of *S. rubra* reduced *S. jonesii* to a forma within *S. rubra.* He noted that many large Coastal Plain individuals lacked *S. jonesii*'s distinctive pitcher taper and he considered these large individuals as belonging to *S. rubra.*

McDaniel (1966) recognized that "*S. rubra*" consisted of more than one morphological form. He states:

> Were almost any taxonomist unaware of the problem given selected specimens from Henderson Co., N. C., and selected specimens from the lower coastal plain of the same state, he would undoubtedly consider the two groups of specimens to represent two clearly distinct species. However, when all of the diversity of *S. rubra* throughout its range is considered, one must conclude that the form common in Henderson County and the form common on the lower coastal plain are extremes of the same species connected by intermediates both in North Carolina and in other states. . . . I believe that this species has basically four morphological expressions, each of which has certain geographic distributions. Intergradation between these forms is common and I do not feel it necessary or desirable to distinguish any or all of them as infraspecific taxa.

Several problems seem to have confused past taxonomists. First is the belief that the *Sarracenia jonesii* leaf form occurs anywhere except in the Carolina mountain counties. Contrary to McDaniel's statement that there are "selected specimens" from the mountains which are the "common" form, there is only one structural form manifested in the mountain counties, *S. jonesii,* and it occurs

only there. Plants from the Fall Line Sand Hills of Alabama represent *S. alabamensis* subsp. *alabamensis,* which produces small *S. rubra*-like spring leaves and large, somewhat *S. jonesii*-like summer leaves. Unusually large plants from the Gulf Coastal Plain represent either large ecads of *S. rubra,* extremes of *S. alabamensis* subsp. *wherryi,* or introgressed hybrid individuals (see discussion elsewhere in this paper).

There remains the problem of the citations of "intergrades" and of the relatively tall sand hill populations from the Carolinas, Georgia and Florida. We have seen no evidence that intergradation occurs at all. The Carolina *Sarracenia jonesii* is not known to make contact with any other members of the *S. rubra* complex. Indeed, it is separated from others of the complex by the Piedmont province which in the Carolinas is approximately 100 miles wide. Large-leaved plants of *S. rubra,* from the inner Coastal Plain and Fall Line Sand Hills, especially the herbarium material from Kershaw, Lee, Lancaster, Chesterfield, and Lexington Counties of North and South Carolina, and plants we collected from Taylor County, Georgia, approach the height of *S. jonesii.* Although they lack the distinctive sharply expanded upper pitcher chamber and the distinctive shape and carriage of the hood, they might easily be interpreted as intermediate forms. To determine if this large-leaf form was genetic or ecological, we collected specimens in the Fall Line hills of Taylor County, Georgia, in 1971 and from near Lucknow, Lee County, South Carolina, on the inner Coastal Plain in 1972. In both areas plants possessed unusually tall pitchers. We grew collected divisions of some of these clones in our comparative culture greenhouses and outside in our sand bog garden. Clones of each area were placed beside plants of *S. jonesii* from Henderson and Transylvania Counties, North Carolina and from Pickens County, South Carolina.

As pointed out by Mandosian (1966) the plants required time to adjust metabolic growth pools. The first leaves produced in cultivation, while smaller than those of *Sarra-*

cenia jonesii, remained larger than typical of outer Coastal Plain Carolina *S. rubra.* Those in the harsher outdoor garden situation became reduced in size most rapidly, but by the end of the third season both the comparative culture plants indoors, and the outdoor plants had reduced leaf size to that typical of outer Coastal Plain *S. rubra,* and all subsequent growth has remained so (see fig. 5). *Sarracenia jonesii,* in both indoor and garden culture has, meanwhile, retained its characteristic leaf shape and leaf size, even though in the outdoor bog garden both moisture and organic matter were below the amounts typical of *S. jonesii* habitat in the wild.

The so-called inner Coastal Plain intermediates between *Sarracenia rubra* and *S. jonesii* thus appear to be nothing more than ecads induced by the generally more shaded, peaty environment.

The disjunct colony of *Sarracenia rubra* in western Florida appears at first to be quite confusing. Within this area occur 1) plants which are typical, 2) plants typical in shape, but taller, and 3) plants much taller, some with rather erect, large, undulate hoods and some with tapered pitchers somewhat resembling those of *S. jonesii.* Particularly in dried specimens, the plants become difficult to place. Some of these unusual plants differ in color as well.

Anderson (1949) has pointed out that certain physical characteristics from one species may pass into another with which it is hybridizing independently of other characteristics, and may become established as a characteristic in the population of the introgressed species in its zone of contact. McDaniel (1966) in chromatographic experiments, suggests that chemical introgression may occur in *Sarracenia* populations where extensive hybridization occurs. He specifically found such evidence between *S. alata* and *S. leucophylla.* He feels (McDaniel, 1966, p. 20) that a degree of variability within certain species may be the result of such introgression. W. H. Camp (1949) published a note on *Sarracenia* in which he expressed the belief that there were no "pure" species in the Gulf Coast regions

at all, only massive hybrid populations. Camp overstated the situation, but hybrid populations abound in the Gulf Coastal Plain.

Along the Yellow River, in Santa Rosa County, Florida, is a mixed *Sarracenia* population in which the following are all fairly common: *S. rubra, S. leucophylla, S. flava, S. psittacina,* and *S. purpurea* subsp. *venosa.* Hybrids, backcrosses, and unusual genetic segregates occur between all species, except between *S. psittacina* and *S. purpurea.* They are most numerous between *S. leucophylla, S. rubra,* and *S. psittacina,* all red-flowered species with seasonal overlap in their flowering in this region. Variation in *S. rubra* here is unusually great. Genes from *S. purpurea, S. leucophylla,* and *S. psittacina* all apparently affect leaf carriage, color, and hood size and shape in *S. rubra.* Some clones from this region and a similar region south of Crestview, Florida, produce pitchers which at first appearance seem to show many of the characteristics of *S. jonesii.* The leaves are taller than those in ordinary *S. rubra,* narrower in their lower portion, and more sharply expanded upwards, with hoods arched higher over the orifice and more reflexed than in other *S. rubra* clones nearby. If one grows these plants and examines the nearly fully expanded but unopened pitchers, he will find small, faint, whitish areoles on the upper pitcher around the orifice and on the back of the hood, evidence of introgressive hybridization with *S. leucophylla. Sarracenia leucophylla* would also account for the unusual height of some of the *S. rubra* introgressants in the region.

Schnell (1974) commented on the large pitchers and the overall red-maroon coloring of many *Sarracenia rubra* plants of this population. One of the most noticeable traits of hybrids involving *S. rubra, S. purpurea, S. leucophylla,* and *S. psittacina* with other species is the presence in well lighted plants of an overall red-maroon flush to the leaf, the red coloring often being more developed than in either parent. F_1 hybrids involving these plants abound in this part of Florida (Bell, 1949, 1952; Bell and Case, 1956) and

most show this deep red coloring. This color, too, we feel has introgressed into the *S. rubra* population where it has enhanced the natural tendency to produce a red flush in the upper pitcher tube.

In bogs south and east of Crestview, Florida, grow large colonies of *Sarracenia rubra* in which the plants are shorter, and less suffused with red, much more in color and size like plants from Georgia and South Carolina. There is much less evidence of hybridization at these locations. Despite minor differences in color and size, and despite the great many unusual individuals, analysis of leaf size and structural features of this western Florida population shows that it most closely resembles the Atlantic Coastal Plain population and we place it in *S. rubra.* Our reconstruction of the group's geological history suggests that the Florida population has descended from the Chattahoochee or Flint River regions of Georgia, a conclusion also supported by our chromatological findings.

2. *Sarracenia jonesii* Wherry, Journ. Wash. Acad. Sci. **19:** 385. 1929.

S. rubra forma *jonesii* (Wherry) Bell, Journ. Elisha Mitchell Sci. Society. **65:** 137. 1949

S. rubra subsp. *jonesii* (Wherry) Wherry. Castanea. **37:** 146. 1972

Largest seasonal leaves of flowering plants 21 to 73 cm tall, elongate at base, tapered, very narrow in lower portion of pitcher tube, becoming widely expanded mostly in the upper ¼ of the tube, often becoming so sharply expanded as to cause a cross-fold or notch-like fold in the adaxial face of the pitcher, with back of pitcher slightly bulged outward, 1 to 4.2 cm wide. Lateral wing of pitcher very narrow, widest below middle of leaf. Leaves firm and waxy textured, green, becoming veined with dark purple, or rarely with an overall deep maroon-black suffusion. Pitcher rim tightly rolled, dark maroon in sunlit leaves, indented somewhat at point where rim and lateral wing join. Hoods

2.4 to 6.5 cm long, 2.4 to 5.4 cm wide, ratio of length/width 0.91 to 1.67, hoods cordate, moderately reflexed, neck contracted, carried rather high over the clearly open orifice, veins of inside of hood colored maroon throughout, leaves semi-evergreen. Flower scapes few-many, erect, rarely exceeding the tallest pitchers of the season, 32.5 to 69.6 cm high. Sepals 2.5 to 3.5 cm long, 1.5 to 2.0 cm wide, broadly ovate, gradually tapered to a blunt tip, maroon or green-maroon mottled. Petals maroon 3.0 to 4.5 cm long, 2.0 to 2.8 cm wide, distal lobe often distinctly shovel-shaped.

Type Locality: Moist meadow 1.5 mi S of East Flat Rock Station, Henderson County, North Carolina, E. T. Wherry.

Type Specimen: U. S. National Herbarium No. 1,438,266. (Wherry).

Distribution: Native only to Buncombe, Henderson and Transylvania Counties, North Carolina, and in Pickens County, South Carolina.

Sarracenia jonesii thrives best in open boggy meadows. It was apparently frequent at one time in such habitats along Muddy Creek, in Henderson County, North Carolina. All known stations there appear to be extinct. Plants from the vicinity of the type locality are generally less heavily colored, and with somewhat shorter, broader pitchers than most of the *S. jonesii* from other stations, and resemble very closely in leaf many Mississippi plants of *S. alata.*

Sarracenia jonesii can also grow in brushy thickets along streams among alders and tangles of *Leucothoe* and other heaths. In such situations six or eight small colonies are known to survive.

Representative Specimens: **North Carolina:** BUNCOMBE CO., mountain bogs, Biltmore, Biltmore Herb. 3374a (NY); Biltmore Estate, *F. E. Boyton* (US); HENDERSON CO., 1½ mi S of Flat Rock, *Wherry* (US); East of Flat Rock, *R. K. Godfrey* (NY); East Flat Rock, *D. Samson* (NY); swamp near R.R. station, Etowah, *E. T. Wherry* (PENN); 1 mi S of East Flat Rock, *Wherry & Pennell* (PH); Hendersonville, *H. H. Jackson* (PH); near Edneyville, *D. S. Correll* (DUKE); TRANSYLVANIA CO., boggy thicket, tributary of Little River, *Case, Moore & Gibson* (US). **South Carolina:** GREENVILLE CO.,

south slopes of Caesar's Head, *Loomis* (PH); south slopes of Caesar's Head, *Case, Moore & Gibson* (US); PICKENS CO. [GREENVILLE CO.?] stream feeding Mt. Lake, *C. R. Bell* (UNC).

Sarracenia jonesii is a rather tall-leaved plant distinguished from others of the *S. rubra* complex in its taller, relatively more slender pitchers having elongate petiole bases with most of the pitcher expansion in the upper quarter of the pitcher tube. Its distinctly cordate hoods are carried rather high over the orifice, and tend to be faintly undulate.

Flower size of vigorous plants of this species can be double that of others in the *Sarracenia rubra* complex, and the distal lobe of the petal tends to be more shovel-shaped than in others of the complex. Under uniform culture conditions the plants bloom about a week after all others of the complex.

Color of leaf and vein develops slowly in this taxon; young leaves seldom exhibit the overall red-maroon flush of developing, well lighted members of other taxa.

Several writers and correspondents have claimed that *Sarracenia jonesii* is merely an ecad of *S. rubra* and that the large, tapered pitchers result from special conditions of moisture, temperature, and light. Our experience indicates that this is a false assumption. We have grown plants of *S. jonesii* alongside *S. rubra* from inner and outer Coastal Plain stations, under identical conditions, for over 20 years. Regardless of the particular ecological conditions, it was the *S. rubra* taxa which varied most and at times became less like their wild counterparts. *Sarracenia jonesii* remained singularly constant and produced the large, sharply expanded pitchers throughout the growing season. Even when deprived of a generous water supply, *S. jonesii* pitchers, although becoming reduced in size, remain distinguishable from those of *S. rubra* in their taper, larger size, hood shape, length of petiolate base, and pitcher wing.

Schnell (1974, p. 8) states "How a plant may vary in different environments as compared to other members of the species which may vary differently or not at all in

transplanting, is still likely biologically significant." We concur, for while we agree that *Sarracenia jonesii* is very close to *S. rubra,* it has maintained its relative differences from that taxon. There can be no question but that these differences are genetic, not ecological.

We consider *Sarracenia jonesii* to be an extremely uniform, constant, relict species confined to the ancient Asheville Peneplain in the Blue Ridge Mountains. We agree with Wherry's assessment (1972) that he originally ascribed too large an area to this species (see discussion under *S. rubra*). The initial confusion led subsequent writers to suppose that the ranges of *S. rubra* and *S. jonesii* overlap, which they do not. The so-called intermediates and intergrades represent other species or unusual ecads of *S. rubra.* It is true that under conditions of deep shade, or if the rhizomes of *S. jonesii* are broken up by cattle trampling, the plants will produce numerous small leaves which overlap in size and shape those of *S. rubra.* Schnell (1974) points out that these are juvenile-type leaves. We agree. If grown under good culture, mature *S. jonesii* produces only tall, flared, distinctive pitchers. Many pitchers of *S. jonesii* cannot be distinguished from similarly sized pitchers of *S. alata* (Wood) Wood. No one seriously considers that *S. jonesii* belongs to that species!

Albino plants occur in at least one locality. This species is truly endangered; it would be a tragedy if its habitat were totally destroyed.

3. *Sarracenia alabamensis* Case & Case, Rhodora 76: 650. 1974.

subsp. *alabamensis.*

Leaves tending to be dimorphic or trimorphic. Spring pitchers smaller, 17.7 to 49.5 cm tall, sigmoidly curved, gradually but regularly tapered from narrow base to a rather broad orifice, 0.7 to 3. cm wide at orifice, clear green to yellow-green, often suffused in upper ⅓ with strawberry-red when young, fading to yellow-green on

hoods. Veins uncolored on outer pitcher surface, strongly maroon-colored within. Lateral wing of pitcher wide, widest at or just below the middle. This highly expanded wing and recurved form of the spring pitcher may represent a transition to a phyllodium. Largest seasonal leaves (summer leaves) produced from early July onward in well lighted and well watered plants, much taller and larger than spring pitchers, 12.2 to 71.7 cm tall, 1.7 to 6.7 cm wide at orifice, densely but finely pubescent, pubescence deciduous in dried material, soft and thin textured, distinctly yellowish-green, often with faint pale yellow-greenish to whitish mottling in upper ¼ of pitcher, resembling obscure areolation — this condition rarely extending onto hood. Hoods of summer leaves large, undulate, with a puckered expansion of tissue between veins; 2.5 to 9 cm long, 2.2 to 8.8 cm wide, strongly and conspicuously reflexed, carried high, low, or irregularly over orifice, strongly apiculate. Rim of pitcher flared-out, loosely rolled, bright yellow-green, lacking maroon overtones, region of juncture of rim and lateral wing strongly indented — almost spout-like. Veins of hood colored only in basal half or not at all. Leaves evergreen only at bases, spring leaves fading and dying as summer leaves produced. Phyllodia produced intermittently, flat, decumbent, recurved, small, usually produced after spring and before summer leaves.

Flower scapes many, even on shaded plants, 27 to 57.2 cm tall, shorter than largest summer pitchers, although exceeding some spring ones, often several produced from one terminal bud. Sepals 2.0-3.0 cm long, 1.2 to 2.0 cm wide, ovate, gradually tapered to blunt end, maroon-green streaked, becoming rather strongly reflexed. Petals variably maroon, usually lighter than in *Sarracenia rubra* or *S. jonesii,* 2.6 to 4.2 cm long, 1.6 to 2.3 cm wide, margins of distal lobe often erose-denticulate. Mature capsules small, 0.6 to 1.0 cm wide.

Type Locality: Elmore Co., Alabama, along the railroad between Elmore and Speigner, Case & Case S-500 (US).

Distribution: In boggy places in the Fall Line Sand Hills (Harper 1922) of Elmore, Autauga, and Chilton Counties, Alabama.

Representative Specimens: **Alabama:** AUTAUGA CO., boggy bank near stream ca 7 mi E of Billingsly, *Case, Gibson and Smith* (US); CHILTON CO., Clanton, *C. L. Pollard & W. R. Maxon* (US); Jasmine, *R. M. Harper* (NY); sloping gravelly bog near Jasmine, *R. M. Harper* (US); gravely bog near Adams, *F. & R. Case, et al.* (US); ELMORE CO., Elmore, *E. T. Wherry* (PENN); 1½ mi S of Speigner, *R. M. Harper* (PH); along the railroad between Elmore and Speigner, *F. & R. Case* (TYPE) S-500 (US).

Sarracenia alabamensis subsp. *alabamensis* is distinct from other members of the *S. rubra* complex in its production of small, usually recurved spring leaves and in the production of few to many large much expanded and voluminous summer and fall pitchers. These summer leaves are yellow-green, almost golden toned, faintly marbled with areole-like pale yellow-green to whitish markings, and with very large, expanded hoods. The spring leaves tend to remain more green-bronze red flushed. Both spring and summer pitchers tend to be short-lived and produced almost continuously during the season if moisture and light conditions are favorable. The plant is a dense clump former and a heavy bloomer.

Since publication of *Sarracenia alabamensis* we have received private communications, some of which suggest that the recurved spring pitchers described in the protologue are not normally produced in nature, but result from poor culture techniques. We have grown this species for 20 years and its behavior with respect to the recurved spring pitchers is consistent. It also produces the spring leaves in the wild (see fig. 8) (fide Thomas Gibson, personal observation, 1975). Plants transplanted to an experimental bog on the estate of C. F. Moore at Brevard, North Carolina, also produced the recurved leaves. *Sarracenia rubra* and *S. jonesii* growing next to this species either indoors or out in our experimental situations do not produce similarly curved spring leaves.

Fig. 8. *Sarracenia alabamensis* subsp. *alabamensis*, showing the large summer pitchers, and a few remaining recurved, smaller, spring leaves. Photograph from a color slide by Thomas Gibson, taken in Chilton Co., Alabama, September, 1975.

We may, in our original description of *Sarracenia alabamensis* subsp. *alabamensis* have emphasized too much the production of laminar phyllodia, for while some plants produce them, production is rare.

In our comparative cultures, *Sarracenia alabamensis* subsp. *alabamensis* blooms after subsp. *wherryi* and *S. rubra*, but before *S. jonesii*.

Since the original publication of this species, we have learned of a few somewhat more extensive colonies than we had previously believed still survived. We have visited one such large meadow colony of over 100 clumps. The geographic range is very limited, and like *Sarracenia jonesii*, the species is a relict in an area where suitable habitat, limited to begin with, and kept open by natural fires, has been rapidly destroyed by human activity. Even though there remain a few meadow colonies of a few hundred plants, most colonies, much smaller, exist only through the accident of habitat kept suitable through moderate pasturing by cattle. Should pasturing cease, the habitats would quickly return to brushy thickets in which, with modern fire protection, the pitcher plant colonies would be shaded out quickly. The species is endangered and deserves managed protection.

4. *Sarracenia alabamensis* subsp. *wherryi* subsp. nova

S. rubra Walter, Fl. Carol. 152. 1778 (in part).

S. jonesii sensu Wherry, Journ. Wash. Acad. Sci. 19: 385. 1929 (in part).

Tota planta subsp. *alabamensi* similis, sed folia vernalia magnitudine et forma foliis aestivalibus similia, 8-45 cm longa, ex rubro viridia, exareolata, ore 0.7-2.8 cm lata. A subsp. *alabamensi* operculis minoribus, suberectis vel orem impendentibus, tam latis quam longis vel latioribus, 0.8-4.5 cm longis, 0.8-4 cm latis, ex cupreo viridibus (non flavo-viridibus), venis viridibus vel coloratis, scapis brevioribus 13.7-45.5 cm altis, differt.

Differs from subsp. *alabamensis* in the following manner: Rhizome: sparsely branching, clump forming tendency only moderate. Pitchers not noticeably dimorphic, petiolate, recurved-ascending; tubular portion more or less erect. Pitchers 8 to 48 cm tall, 0.7 to 2.8 cm wide at orifice, often stout, frequently very gradually tapered from the base to orifice, not flared, but with the pitcher taper widest below the orifice. Pitchers densely fine pubescent, green to bronze-green, upper portion and hood flushed salmon-pink, external veins mostly without dark maroon coloring, major veins dark maroon-purple within (dark color may show through giving a false impression of coloring in external veins, especially in dried specimens). Hoods wider than long, variable, convex and weakly reflexed in most plants from the southwestern corner of the range, more erect, reflexed and with undulate margins in the northern and northeast corner of its range; veins of the underside of the hood heavily colored maroon-red in the neck and proximal portion, uncolored to colored only on a few of the main veins extending into the hirtellous distal region, veins of hood exterior scarcely if at all colored. Pitcher rim not flared out, moderately outrolled, yellow-green, moderately indented at juncture of orifice rim and lateral wing.

Flowers very early, scapes short, 13.7 to 45.5 cm tall, produced before development of pitchers, and barely equaling or exceeding pitchers; relatively large, 3.9-6.1 cm wide. Petals maroon-red often yellow streaked or orangish, but dark red-maroon in northeast portion of its range, distal lobe strongly obovate. Sepals broad, not strongly reflexed, 2.3 to 3.0 cm long, 1.5 to 2.0 cm wide, bluntly rounded. Style umbrella 3.2 to 4.2 cm wide, the divided tips of the lobes rounded at their apex.

TYPE: Common along a swampy trough in the pine woods about ½ mile east of Chatom, Washington Co., Alabama, growing with *S. leucophylla* Raf. *F. & R. Case* S-573 (US), collected July, 1972, but prepared from cultivated material in September, 1974.

Distribution: Northern Baldwin Co., western Escambia Co., and Washington Co., Alabama, and Wayne Co., Mississippi.

Representative Specimens: **Alabama:** Baldwin Co., 12 mi E of Bay Minette, *S. T. McDaniel* (FSU); Bay Minette, *J. M. MacFarlane & C. Goesty* (PENN); 10 mi N of Bay Minette, *LeClair* (UNC); WASHINGTON CO., damp pine barren between Chatom and Deer Park, *R. M. Harper* (NY); 3 mi NW of Fruitdale, *S. T. McDaniel* (FSU); 4.5 mi W of Chatom, *S. T. McDaniel* (FSU); 4 mi N of Deer Park, *S. T. McDaniel* (FSU); 10 mi N of Citronelle, *S. T. McDaniel* (FSU); swampy trough in pine woods, ½ mi E of Chatom, *F. & R. Case* S-573 (Type). **Mississippi:** WAYNE CO., Waynesboro, *C. L. Pollard* (NY), (US).

Sarracenia alabamensis subsp. *wherryi* occurs in the pineland bogs of Wayne Co., Mississippi, Washington County, Alabama and east of the Tombigbee and Alabama River systems, much more sparingly in northern Baldwin and western Escambia Counties, Alabama.

This subspecies is locally abundant in ditches and pineland bogs in the western parts of its range, yet it seems not to have penetrated very far into Mississippi, nor to have reached the rich *Sarracenia* bogs southwest of Mobile, Alabama.

We dedicate this subspecies to Dr. Edgar T. Wherry, whose insights into Sarraceniaceae are particularly clear, and who has been so generous with his time, information and assistance to professional and amateur botanists alike.

Sarracenia alabamensis subsp. *wherryi* has pitchers much like the spring leaves of subsp. *alabamensis* in color, pubescence, texture and markings. The pitchers, however, lack the sigmoid curve so common in spring leaves of subsp. *alabamensis*, and tend to be recurved only in the petiolate base. Summer pitchers are of the same sort as the spring ones and only slightly larger; they lack the strong yellow undertones and obscure whitish areolations. Flowers in this taxon are larger, on shorter stems, with very obovate petals, and fewer are produced per plant.

Whereas the majority of plants of this population are quite distinct, some plants resemble plants of the Florida

population of *Sarracenia rubra* in general size and shape. Although there is no herbarium evidence of contact between these two populations, and we have found no evidence in our field work, the distance between the populations is not great and some gene flow between them could have occurred which might account for some of the similarities. However, the eastern segment of the population of subsp. *wherryi* varies less; many of the plants which most closely approach *S. rubra* here grow in the western edge of the area, in southern Washington Co., Alabama, where hybridization with *S. alata* and others is rampant. We are inclined, therefore, to believe these confusing plants have resulted from introgressive hybridization with *S. alata, S. psittacina* and *S. leucophylla* rather than from intergradation with *S. rubra.*

Since leaf substance, pubescence, general shape and volume, color and hood features of subsp. *wherryi* are most similar to the same features in comparable leaves of *Sarracenia alabamensis;* since the populations occur partly on the same river system, separated only by 100 miles of unsuitable Black Belt soils; and because plants from this population from near Perdido, Alabama, when chromatographed shared in common with most plants of subsp. *alabamensis* a flavonoid compound not found in others of the *S. rubra* complex, we place this plant as a subspecies of *S. alabamensis* while we acknowledge that its origin could be more complex.

GEOLOGICAL HISTORY AND SPECULATION

In his "Distribution of North American pitcher plants", Wherry (1935) theorizes that our modern sarracenias originated on the old pre-Cretaceous [Schooley or Cumberland (Fenneman, 1938)] peneplain of eastern North America somewhere between the limits of glaciation and the present day Fall Line. At that time, our present day Coastal Plain did not exist, but authorities agree that conditions of moisture and climate on the old peneplain

were fairly similar to modern-day conditions on the Coastal Plain (Wherry, 1935; Braun, 1950). Tertiary uplifts later created the present Applachian-Cumberland regions, destroying the old boggy peneplain conditions, while the resulting erosion deposits and crustal movements caused development of the Coastal Plain lowlands. As most suitable *Sarracenia* habitat in the Tertiary uplands was slowly destroyed, the plants presumably spread down onto the developing Coastal Plain which is their center of occurrence today.

Wherry's generalized account agrees well with the theories and evidence presented by other plant-geographers (Cain, 1944). In the study of relict species on the Blue Ridge or Cumberland Plateau of plants very local there and more abundant on the Coastal Plain, *Sarracenia* is often cited.

With so much attention having been given to the geological history of this region, it is interesting that no one has previously examined this history in relation to the *Sarracenia rubra* complex. Each of the major disjunct populations of the *S. rubra* complex centers around the swamps of a major river system which today has or in the past has had its headwaters in or very near to Henderson, Transylvania or Buncombe Counties, North Carolina, and Pickens and Greenville Counties, South Carolina, or can be shown to have had headwaters connections in the past into the French Broad-Tennessee River region just west of the Great Smoky Mountains. In that region of the western Carolinas, an ancient strath or peneplain (Asheville Peneplain, Fenneman, 1938) survived largely intact the geological upheavals which destroyed most of the pre-Cretaceous peneplain elsewhere in the region (Fenneman, 1938). Especially at its southern end, the incipient peneplain lacked sharp drainage (Fenneman, 1938). That it remained suitable for pitcher plants is evidenced by the presence there today of *S. jonesii* and *S. purpurea.* Three major rivers pertinent to this study arise in this area, the Chattooga, Saluda, and the French Broad. Headwaters of

the Catawba, Peedee and Cape Fear Rivers arise just over the divides to the east and northeast.

One may speculate as follows upon the past events. The common ancestor of the modern *Sarracenia rubra* complex survived the Tertiary Uplifts in the ancient Asheville Strath. In the early history of this region, the Chattooga River was continuous with the Chattahoochee River (via Deep Creek, Fenneman, 1938). There was, therefore, a past direct corridor from the ancient mountain strath bogs to the Fall Line hills habitat of western Georgia, over which pitcher plants or their propagules might migrate. Along this route, and across divides of only a few miles lie the headwaters of the Flint and Ocmulgee Rivers where *S. rubra* grows today. From these sand hill regions migration downstream and across rather narrow divides could have taken place from the lower Chattahoochee to the southwestward flowing rivers which drain the area just east of Pensacola, Florida, where the disjunct colonies of *S. rubra* occur on the Coastal Plain today.

At a later time, the upper Chattahoochee (Chattooga) was captured by the headward growing Savannah River (Fenneman, 1938, p. 136-137) and the westward shift of the Blue Ridge divides as the east coast rivers with steeper gradients extended their headwaters (Fenneman, 1938, Dietrich, 1971). A series of migration corridors, direct via the Chattooga-Savannah Rivers, and somewhat less direct, through the westward shift of the Blue Ridge divides (Fenneman, 1938), opened up to the Atlantic Coastal Plain swamps. That it is possible for pitcher plants to cross this Blue Ridge divide along these streams is attested to by the presence of "cataract colonies" (Wherry's term) of *Sarracenia jonesii* along streams draining to the Atlantic today at an elevation well below the elevation at which the bulk of the *S. jonesii* population grows in its main range west of this divide in the French Broad (Mississippi) drainage.

In this manner, apparently, the ancestor of the present eastern *Sarracenia rubra* migrated from this mountain

area into the drainages from eastern Georgia to the Cape Fear River. Limited lateral spreading through the outer Coastal Plain swamps probably occurred in this area.

West of the Coosa in Alabama grow *Sarracenia alabamensis* subsp. *alabamensis* and subspecies *wherryi*. Evidence of the early history of these taxa is less direct. The Coosa drains from the Great Valley region (Fenneman, 1938) between the Tennessee River and the Great Smoky Mountains, near the Tennessee-Georgia state line, but has tributaries from the east which reach nearly to the Chattahoochee. The French Broad River, older than the Appalachians (Fenneman, 1938), crosses them and flows through the Great Valley to the Tennessee. Although postulated by some authorities, a direct connection from the Tennessee River to the Coosa has not been demonstrated.

It is possible that the ancestor of *Sarracenia alabamensis* originated in the area occupied by *S. jonesii* today, and that it reached the Coosa headwaters either via the French Broad drainage along which today the bulk of the *S. jonesii* population occurs, or via the Chattahoochee corridor to the lower Coosa tributaries.

Since *Sarracenia alabamensis* differs more from *S. jonesii* and *S. rubra* than the latter two differ between themselves, it seems most likely that before the Tertiary uplifting, a common ancestor to the *S. rubra* complex occurred not only in the Asheville Peneplain, but in the regions farther west of the Great Valley and Cumberland Plateau. This ancestral stock became separated by the events which formed the Appalachian Mountains and in the west became obliterated. Before the western form became extinct in the Cumberland Plateau region, some of its members reached the headwaters of the Coosa and descendents found their way to the Fall Line Sand Hills of Alabama where they survive in a limited area today.

At a later date descendents of this population crossed the Black Belt soil barrier and evolved into subsp. *wherryi* near the Alabama and Tombigbee Rivers north of Mobile Bay.

In the course of the long history involved in these migrations, the localized, isolated populations became changed from one another, perhaps through genetic drift, mutation, and hybridization with other species.

That this has been the method of development of the *Sarracenia rubra* complex, rather than through the extinction of parts of a once more or less continuous Coastal Plain or Fall Line population, is evidenced in several ways: those populations which occur on the same or a historically related river system resemble each other structurally more than do those members of the complex on river systems with a different history; the absence of *S. rubra* from many Coastal Plain swamps which are, however, occupied by other species of sarracenias (i.e., *S. flava, S. leucophylla, S. psittacina*), suggests to us not that the former Coastal Plain range of *S. rubra* has been reduced, but rather that members of the *S. rubra* complex have descended from an ancient stock which during the Tertiary times became broken into small, isolated populations which have become so adapted to their particular habitats that they lack the genetic aggressiveness to colonize extensively.

All members of the *Sarracenia rubra* complex are extremely winter hardy. We grow all species of *Sarracenia* outdoors at Saginaw, Michigan, where winter temperatures (often without snow cover) commonly fall to minus 18°C, and may reach to minus 30°C. Such a degree of hardiness suggests to us a more upland or interior developmental history rather than an origin on the rather mild Coastal Plain.

Of particular interest is a finding from the chromatographic study of this complex. Several "pairs" of disjunct populations share flavonoid compounds which were not generally present in other populations of the complex (see Table 3).

In each instance, the population on the geologically younger Coastal Plain occupies swamps in the vicinity of a major river system which drains from an older, Fall Line or Blue Ridge region occupied by the other population with

TABLE 3

Inland, Geologically older Fall Line or Blue Ridge Region		Outer Coastal Plain, Geologically Younger Region
S. jonesii, Western Carolinas	←→	*S. rubra*, Western Florida
S. rubra, Taylor Co., Georgia	←→	*S. rubra*, Western Florida
S. jonesii, Pickens & Buncombe Counties, S. & N. Carolina (but not all *S. jonesii* tested)	←→	*S. rubra*, Carolina Coastal Plain.
S. alabamensis subsp. *alabamensis*, Chilton, Autauga, Elmore Cos., Alabama	←→	*S. alabamensis* subsp. *wherryi*, vicinity of Perdido, Baldwin Co., Alabama

Table 3. Regions of occurrence of *Sarracenia rubra* complex taxa which share a flavonoid compound which is not generally present in the other populations of the complex.

which it shares a compound. The presence of a compound not found elsewhere in the *Sarracenia rubra* complex in two disjunct populations on the same river drainage system suggests to us a relationship between them which supports our construction of the group's history. It does not seem likely to us that coincidence could account for all of the compound sharing pairs of disjunct populations to occur on just the "right" river systems to fit our historical reconstruction.

When all the evidence is considered, we believe that the species which constitute the *Sarracenia rubra* complex derive from a common pre-Cretaceous ancestral stock which became discontinuous due to Tertiary geological events. Two surviving segments of the original ancestral population, one east and one west of the Appalachians, managed to migrate along definite routes to Fall Line or Coastal Plain areas. Another descendant survived in the ancestral Blue Ridge home area as well. During the course of these events, the various populations have diverged to form three closely related species.

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LITERATURE CITED

ANDERSON, E. 1949. Introgressive hybridization. John Wiley & Sons, N.Y. 109 pp.

BELL, C. R. 1949. A cytotaxonomic study of the *Sarraceniaceae* of North America. Jour. Elisha Mitchell Sci. Soc. **65**: 137-166. *Pls.* 8-14.

————. 1952. Natural hybrids in the genus *Sarracenia.* I. History, distribution and taxonomy. Jour. Elisha Mitchell Sci. Soc. **68**: 55-80.

BELL, C. R. & F. W. CASE. 1956. Natural hybrids in the genus *Sarracenia.* II. Current notes on distribution. Jour. Elisha Mitchell Sci. Soc. **72**: 142-152.

BRAUN, E. L. 1950. Deciduous forests of eastern North America. Blakiston Co., Philadelphia. 596 pp.

CAMP, W. H. 1949. A note on *Sarracenia.* Bull. Torrey Bot. Club. **76**: 10-11.

CAIN, S. A. 1944. Foundations of plant geography. Harper & Bros., N. Y. 556 pp.

CASE, F. W. & R. CASE. 1974. *Sarracenia alabamensis*, a newly recognized species from Central Alabama. Rhodora **76**: 650-665.

DIETRICH, R. V. 1971. V=f(S . . .), pp. 67-99. *In:* Holt, P. C. (ed.). The distributional history of the biota of the Southern Appalachians. Part II. Flora. Research Div. Monograph 2. Virginia Polytechnic Inst. and St. Univ., Blacksburg, Va.

FENNEMAN, N. M. 1938. Physiography of eastern United States. McGraw-Hill, N. Y., N. Y. 714 pp.

HARPER, R. M. 1918. The American pitcher plants. Jour. Elisha Mitchell Sci. Soc. **34**: 110-125.

————. 1922. Some pine-barren bogs in Central Alabama. Torreya **22**: 57-59.

HECHT, A. 1949. The somatic chromosomes of *Sarrecenia.* Bull. Torr. Bot. Club. **76**: 7-9.

MACFARLANE, J. M. 1908. *Sarraceniaceae. In:* A. Engler, Das Pflanzenreich. **4**: pt. 110.

MANDOSSIAN, A. J. 1966. Variations in the leaf of *Sarracenia purpurea* (Pitcher plant). Mich. Botanist. **5**: 26-35.

MCDANIEL, S. T. 1966. A taxonomic revision of *Sarracenia* (*Sarraceniaceae*). Unpubl. Ph.D. Diss., Fla. S. Univ.

————. 1971. The genus *Sarracenia* (*Sarraceniaceae*). Bull. Tall Timbers Research Station. **9**: 36.

PLUMMER, G. L. & J. B. KETHLEY. 1964. Foliar absorption of amino acids, peptides and other nutrients by the pitcher plant, *Sarracenia flava.* Bot. Gaz. **125**: 245-260.

SCIENCE NEWS. 1974. **106**: 286.

SCHNELL, D. E. 1974. The kaleidoscope of *Sarracenia.* Carniv. Plant Newsletter **3**: 7-10.

WALTER, T. 1788. Flora Caroliniana, pp. 152-153. J. Wenman, London.

WHERRY, E. T. 1929. Acidity relations of the Sarracenias. Jour. Wash. Acad. Sci. **19**: 379-390.

————. 1933. The geographic relations of *Sarracenia purpurea.* Bartonia **15**: 1-6.

————. 1935. Distribution of the North American pitcher plants. In M. V. Walcott, Illustrations of North American pitcher plants. Smithsonian Inst., Washington, D. C.

————. 1972. Notes on *Sarracenia* subspecies. Castanea **37**: 146-147.

7275 THORNAPPLE LANE
SAGINAW, MICHIGAN 48603

AN UNUSUAL BLACK GUM SWAMP IN MAINE: Stands of black gum, *Nyssa sylvatica* Marsh., are infrequent in northern New England. Where they occur they appear to be confined to hummocky swamps of only a few acres. These swamps and their associated vegetation are quite striking and contrast sharply to the typical northern hardwood forests on the surrounding uplands. The deeply fissured black trunks of old gum trees standing among beds of lush green ferns give the swamps a character which does not seem real for northern regions. One such gum swamp in Vermont was described some years ago (Vogelmann, 1969; Fosberg, 1970).

During the summer of 1974 I visited an outstanding example of a black gum swamp in New Gloucester, Maine. About 5 acres of hummocky swamp is located near the summit of Little Hill at an elevation of 500 feet. Although the surrounding forests have been heavily cut-over, the black gum stand in the swamp is nearly untouched. Only several cut stumps were found near the edges, and for all practical purposes the stand is virgin.

Nyssa sylvatica dominates the area and about 60 trees over 12 inches d. b. h. were counted. Trunks of some of the large trees are 22-23 inches in diameter with bark fissures deep enough to put a hand into. Taller trees reach to about 80-90 feet, and one fallen tree 17 inches d. b. h. measured 60 feet to its broken top which was 6 inches in diameter at that point. The trees appear remarkably healthy and vigorous. Smaller trees with stems under 4 inches in diameter are scarce.

Tsuga canadensis (L.) Carr. is fairly abundant with trunks of the larger trees up to 30 inches d. b. h. *Acer rubrum* L., up to about 10 inches d. b. h., is common and some *Betula alleghaniensis* Britton is scattered in the swamp. A few *Picea glauca* (Moench) Voss. are present and there are a number of seedlings of *Pinus Strobus* L. and *Quercus rubra* L. on the hummocks.

The shrubby understory is comprised largely of *Nemopanthus mucronata* (L.) Trel., *Vaccinium corymbosum* L. and *Viburnum cassinoides* L. Other shrubs include *Kalmia*

angustifolia L., *Rhododendron canadense* (L.) Torr., *Alnus rugosa* (De Roi) Spreng. and *Pyrus floribunda* Lindl.

Pools of water are interspersed among the hummocks and mossy logs are scattered about. Sphagnum moss dominates the hummocks along with *Osmunda cinnamomea* L., *Maianthemum canadense* Desf., *Aralia nudicaulis* L. and *Clintonia borealis* (Ait.) Raf. are common on the mounds. Also found here are *Trientalis borealis* Raf., *Coptis groenlandica* (Oeder) Fern., *Smilacina trifolia* (L.) Desf., *Gaultheria procumbens* L. and *Rubus hispidus* L. Near the edges of the swamp are mucky pools with *Iris versicolor* L., *Carex* cf. *brunnescens* (Pers.) Poir. and *Dryopteris Thelypteris* (L.) Gray.

The sloping rim surrounding the black gum swamp supports a heavy growth of *Hamamelis virginiana* L. and *Fagus grandifolia* Ehrh. Beyond the rim the dense cut-over forests are dominated largely by *Acer rubrum* L. and *Betula alleghaniensis* Britt.

Mr. Warner Chandler of New Gloucester, one of the owners of the swamp, gave me a piece of black gum wood taken from a tree he had cut near the edge of the stand. The growth rings are very close and 177 rings were counted on a 4 inch section. Since the larger trees have trunks about 23 inches in diameter the ages of some trees could be in excess of 400 years, which must place them among the oldest trees in Maine. These calculations assume uniform growth rates and allow for a 2 inch thickness of bark.

The ecology and flora of the black gum swamp in New Gloucester, Maine, is remarkably similar to the gum swamp described in Vermont. Black gum near its northernmost range limits seems to be confined to a unique well-defined habitat. A comparison of the flora and ecology of similar old age black gum stands in New England would be useful to determine if these relic stands are indeed as similar as they appear to be.

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THE BIOSYSTEMATICS OF CARDAMINE BULBOSA (MUHL.) B.S.P. AND C. DOUGLASSII BRITT.

THOMAS W. HART AND W. HARDY ESHBAUGH[1]

In his classic monograph of the genus *Cardamine,* Schulz (1903) considered *C. douglassii* to be a variety of *C. bulbosa.* Since then, most taxonomists, including Deam (1940), Fernald (1950), Gleason (1952), Gleason and Cronquist (1963) and Stuckey (1962) have considered them to be two separate species. However, the difficulty in distinguishing these two taxa is well documented in the literature.

Schulz (1903) split *Cardamine rhomboidea,* including *C. douglassii* and *C. bulbosa,* into two major varieties. Variety *pilosa* was characterized by small amounts of pubescence at the base of the stem and on the leaf margins while variety *hirsuta* had pubescence covering the whole plant including the sepals. Each variety was further subdivided into two sub-varieties based on petal size. These varieties also seemed to vary in leaf shape causing Schulz (1903) to recognize three distinct forms. In none of these forms or varieties was flower color or length of pubescence mentioned. Although the name *C. douglassii* and its synonyms (Torrey, 1822; Gray, 1848; Britton, 1889) was known to Schulz (1903), he ignored the taxon itself. Most,

[1]Financial support of this investigation was provided by the society of the Sigma Xi with a grant to T. W. Hart and by the National Science Foundation through Grant GB 27747 to both of the authors.

but not all, of the purple flowered plants which Schulz observed were considered as the hirsute variety with large flowers. Most of the white flowering plants were considered as the pilose variety with small flowers.

Fassett (1940) considered the basal leaves of *Cardamine bulbosa* to be longer than wide and diagnostic in separating that taxon from *C. douglassii*. While there appears to be too much overlap between the two taxa for this to be a good distinguishing character (Stuckey, 1962) it may be used at times. The presence of a red-purple cast to the underside of the basal leaves of *C. douglassii* and the usual lack of this pigmentation on the leaves of *C. bulbosa* has also been considered as a diagnostic character (Stuckey, 1962). However, in this study it was found that any characters involving basal leaves should be avoided since by flowering time both species, especially *C. bulbosa*, lack their lower leaves. It was also noted that under conditions of high light intensity both species have purple undersides of the basal leaves.

Deam (1940) and Easterly (1967) found the length of the pod and the length of the beak too variable to be of taxonomic value. The external morphology of the seeds reveals no reliable differentiating characters separating the two species (Murley, 1951).

Several workers (Gleason & Cronquist, 1963; Easterly, 1964, 1965) have separated these two taxa by flower color with *Cardamine bulbosa* usually having white flowers (Farwell, 1925; Deam, 1940; Stuckey, 1962). Hitchcock and Standley (1919) and Stuckey (1962) report that sepal color is less variable than petal color and, therefore, a better character.

According to Braun (personal communication) these taxa are ecologically separated. However, Stuckey (1962) has found both taxa blooming at different but overlapping times, and growing sympatrically in association with supposed interspecific hybrids.

The ranges of *Cardamine bulbosa* and *C. douglassii* are quite similar in the northern areas. The northern boundary

for both appears to be New Hampshire, southern Ontario to central Michigan, and southern Minnesota (Fernald, 1950). *Cardamine bulbosa* extends west to eastern South Dakota, Kansas and Missouri, and as far south as Texas and central Florida. *Cardamine douglassii,* however, is more northern in that its southern range is from Missouri to Tennessee and Virginia. According to A. J. Sharp (personal communication), *C. douglassii* is rather rare in Tennessee and seems to be limited to calcareous soils in that region.

Stuckey (1962) concluded that these two species could best be distinguished by a combination of characters, including their different flowering periods, pubescence length, sepal color, number of branches, number of cauline leaves, and height to the lowest pedicel. He suggested that the best morphological character for separating these two taxa is the length of the stem pubescence.

Stuckey has since considered separating *Cardamine bulbosa* into two varieties as did Schulz (1903), based on the amount of pubescence (Stuckey, personal communication). He has plotted the distribution of the two forms in Ohio (unpublished data, 1966) and found that the pubescent forms are more common in eastern and southern Ohio while the near glabrous forms are found most often in northern and western Ohio.

If separate taxa are to be recognized, Stuckey's investigations (1962, 1967) have clearly established the correct nomenclature for these two species as *Cardamine bulbosa* (Muhl.) B.S.P. and *C. douglassii* Britton. Nonetheless, the question remains as to whether these are indeed two distinct taxa. In an attempt to answer this question we initiated an investigation into the biosystematics and evolution of *C. bulbosa* and *C. douglassii.*

CHEMOSYSTEMATICS

The distributional pattern of the flavonoid glycosides in both *Cardamine douglassii* and *C. bulbosa* was examined

as a possible means of differentiating between taxa and detecting cryptic phenotypic differences. A search of the literature has not revealed any previous chemosystematic work on any of the North American members of *Cardamine* or *Dentaria*. However, Grouville, Egger and Pacheco (1970) have identified Kaempferol glucosides in *C. pratensis* of Europe.

Two dimensional paper chromatography was applied to populations of both *Cardamine douglassii* and *C. bulbosa* as a possible means of differentiating between the two taxa (Table 1). Three to five (about 0.2 g) air dried cauline leaves from mature plants were soaked overnight in 50% acidified aqueous methanol. The total methanolic extract was then spotted directly onto Whatman No. 3 MM paper (46 × 57 cm). Sixty-two chromatograms representing 14 populations were included in this study (Hart, 1972; Appendix 5).

The descending method was used to develop the chromatograms. They were first developed in the long direction using tertiary-butyl alcohol, acetic acid, and water (3:1:1, v/v; TAW) and then in the short direction in acetic acid and water (5:95, v/v; HOAc) (Mabry, Markham & Thomas, 1970). After drying, the chromatograms were examined under transmitted long wave ultraviolet light with and without ammonia vapors. Most flavonoid glycosides appear as dark purple light absorbing spots in ultraviolet light and fluoresce yellow to yellow-green with ammonia vapor in ultraviolet light (Mabry, Markham & Thomas, 1970).

Partial characterization of the flavonoids was attempted with Benedict's reagent which distinguishes between monohydroxy and orthodihydroxy flavonols by forming a copper complex between adjacent hydroxyls (Seikel, 1962). This flavonol-copper complex appears dark in reflected ultraviolet light while flavonoids lacking adjacent hydroxyls appear as various shades of yellow to yellow-green.

Hydrolysis and analysis of methanolic extracts for glycoflavone (O-glycosyl flavonoid) determination followed

TABLE 1. POPULATIONS STUDIED MORPHOLOGICALLY (M), ECOLOGICALLY (E), AND CHEMICALLY (C)

Species	Location and characteristics	(M)	(E)	(C)
*C. bulbosa**	Mammoth Cave, Kentucky growing in cold spring water	1	L	Race A
C. bulbosa	Pulltight Springs, Missouri growing in cold spring water	2		Race B
C. bulbosa	Buckeye Lake, Ohio edge of floating acid bog	3	U	
C. bulbosa	Blue Ash, Ohio (near Cincinnati) swamp and moist woodland	4	P	Race C
C. bulbosa	Hueston Woods State Park, Oxford, Ohio; moist woodland *C. douglassii* nearby	5	H	Race A
C. bulbosa	Madeira, Ohio (Cincinnati Country Day School) wet woodland	6	O	Race C
C. bulbosa	Spring Valley, Ohio swamp	7	Q	Race C
C. bulbosa	Spring Valley, Ohio open marsh	8	R	Race C
C. bulbosa	Cedar Bog near Springfield, Ohio swamp (northern tendencies)	9	T	Race A
*C. bulbosa**	Mammoth Cave, Kentucky moist woods (very dry when compared to other *C. bulbosa* habitats)	10	N	
C. bulbosa	Pymatuning State Park, Andover, Ohio	11	V	
C. bulbosa	Bowling Green, Ohio; wet woodland (large numbers of *C. douglassii* nearby and putative hybrids)	12	A	Race A
C. bulbosa	Mammoth Cave, Kentucky drainage from a cold spring (Cooper Springs)		M	
C. bulbosa (Hybrid)	Camp Hook, Franklin, Ohio swamp (*C. douglassii* nearby)		S	

Species	Location and characteristics	(M)	(E)	(C)
C. bulbosa	Madeira, Ohio (Cincinnati Country Day School) mowed (periodically) moist field not used in analysis of woody plants		W	
C. douglassii/ C. bulbosa	Bowling Green, Ohio wet woodland (HYBRIDS)		B	Race A
*C. douglassii**	Bowling Green, Ohio; wet woodland (some *C. bulbosa* nearby with putative hybrids)	13	A	Race A
C. douglassii	Camp Hook, Franklin, Ohio wet to moist woodland (*C. bulbosa* nearby, one putative hybrid found)	14	C	Race A
*C. douglassii**	Bedford, Ohio moist woodland	15	E	
C. douglassii	Spring Valley, Ohio woodland along lake shore *C. bulbosa* nearby	16	F	Race A
C. douglassii	Rush Run Wildlife Area, Somerville, Ohio disturbed woodland	17	G	
C. douglassii	Hueston Woods, Oxford, Ohio moist woodland (*C. bulbosa* nearby)	18	H	Race A
C. douglassii	John Bachelor Preserve, Oxford, Ohio; moist-dry woodland (*C. bulbosa* and one clump putative hybrids found)	19	J	Race A
C. douglassii	Spring Valley, Ohio moist lake shore *C. bulbosa* nearby	20	K	
C. douglassii	Camp Hook, Franklin, Ohio wooded hillside (*C. bulbosa* at bottom of hill)	14	D	
C. douglassii	John Bachelor Preserve, Oxford, Ohio; wooded hillside		I	

(12) this population was not included in the morphological study
* $n = 48$, all others presumably $n = 32$

Wagner's (1966) method and standard spectroscopic methods were used for the characterization of key compounds (Mabry, Markham & Thomas, 1970; for details see Hart, 1972).

The chromatographs representing the fourteen populations of *Cardamine douglassii* and *C. bulbosa* studied reveal eighteen putative flavonoid glycosides. These spots are numbered arbitrarily in Figure 1. The composite chromatograph (Fig. 1) also reveals that the spots can be segregated in such a fashion as to reveal three or four distinct categories or races.

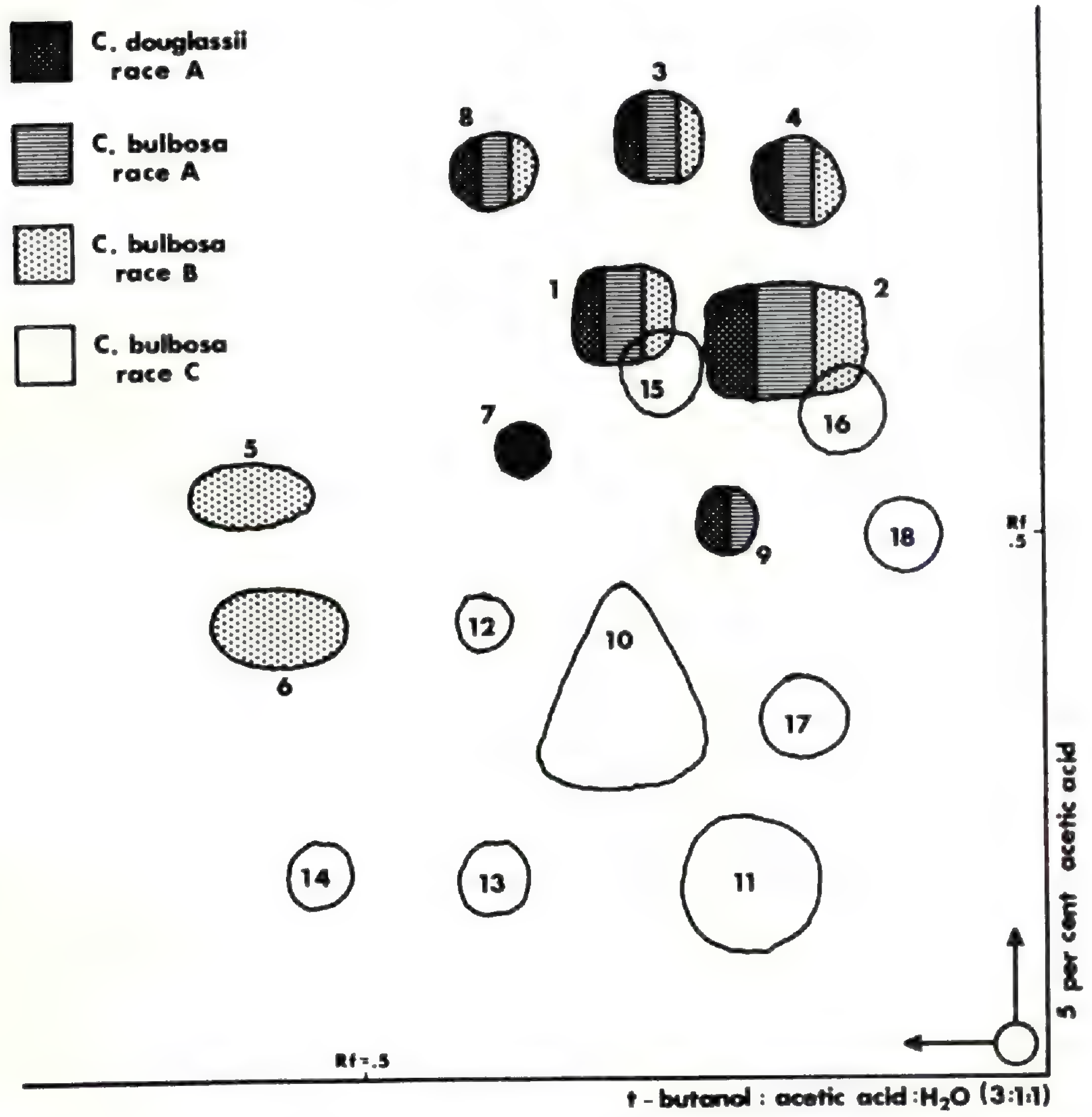


Fig. 1. Diagrammatic sketch of the chromatographic patterns shown by the chemical races in *Cardamine bulbosa* and *C. douglassii.*

Absorption maxima and colors for the spots studied have been characterized (Table 2). These data indicate that they are indeed flavonoids. Acidic hydrolysis of the compounds is easily accomplished indicating that all spots studied are flavonoid O-glycosides. Authentic samples of a few flavonoids were available for comparison with the experimental compounds. Mabry, Markham and Thomas (1970) illustrated a large number of flavonoid spectra obtained by these techniques which reinforced the identification of these compounds.

Spot 10, which is found in very large amounts in the populations of *Cardamine bulbosa* (Race C), is tentatively identified as a Quercetin 3 glycoside. The compound appears dark in Benedict's indicating two hydroxyls on the B-ring. The presence of 7-hydroxyl is shown by the bathochromic shift of Band II in sodium acetate. Both Band I and II show a shift in sodium hydroxide which is indicative of a free 5-hydroxyl. Since this compound is stable in alkaline solutions and exhibits a methanolic peak at 360 nm. it is a flavonol, with the sugar attached at the 3-position. Spot 17 has a similar spectrum (Table 2) and may also be a Quercetin 3 glycoside, possibly differing from spot 10 by having an additional or different sugar.

Spots 3, 4 and 8 have the same spectra in *Cardamine douglassii* and in *C. bulbosa* (Race A). Since these compounds have one hydroxyl in the B-ring (light in Benedict's solution) and a methanol Band I maxima of 349 nm. they are most likely Kaempferol derivatives. The lack of shifts of Band II in the sodium acetate spectra is evidence that the 7 positions are blocked. As the compounds do not break down in sodium hydroxide, the 3-position must be substituted. Therefore, spots 3, 4 and 8 are tentatively identified as Kaempferol 3-7 glycosides which probably vary from each other in the number and types of sugar substitution. Spots are found in the same location in Race B and are probably the same compound.

Spot 11 in Race C has tentatively been identified as luteolin-7-glycoside. This compound is dark in Benedict's

solution indicating the presence of two hydroxyls on the B-ring. The lack of a shift of Band II in sodium acetate is indicative of a blocked 7-position. The methanolic Band I maximum of 340 nm. indicates that the compound is a flavone.

The *Cardamine bulbosa/C. douglassii* complex may, under further investigation, turn out to be highly variable chemically. Present work reveals as many as three chemical races present among the plants studied (Fig. 1). The absence of one or two spots may, in this preliminary study, be looked upon as inconclusive. Since only 62 chromatograms were included in this study with as few as five chromatograms examined in one race, the lack of a spot may be due to its presence in a small undetected concentration.

All *Cardamine douglassii* populations studied and many midwestern *C. bulbosa* populations (Race A) appeared to have similar patterns of flavonoid constituents. One additional spot (no. 7) may be present in *C. douglassii;* however, its absence in *C. bulbosa* (Race A) has not been satisfactorily substantiated.

It is assumed that compounds 1 and 2 are different from compounds 15 and 16. This is indicated for compounds 1 and 15 (Table 2) which shows that the aglycones derived from spot 1 in *Cardamine douglassii* and *C. bulbosa* (Race A) have similar aglycone spectra while the aglycone from compound 15 of *C. bulbosa* (Race C) appears different. A similar situation occurs with compounds 2 and 16 (Table 2). In addition, *C. bulbosa* (Race C) differs from the other races in the presence of 7 dark absorbing compounds having a placement completely different from the spots in the other races (Fig. 1). Spot 10 (Quercetin 3 glycoside) of *C. bulbosa* (Race C) is always very concentrated, so much so that it normally stains the paper yellow in white light.

Cardamine bulbosa (Race B) is characterized by the presence of two dark absorbing compounds (Fig. 1) not found in the other races (nos. 5 and 6). Spectral analysis

TABLE 2. DIAGNOSTIC CHROMATOGRAPHIC ATTRIBUTES AND ABSORPTION MAXIMA OF FLAVONOID CONSTITUENTS ISOLATED FROM *CARDAMINE BULBOSA* AND *C. DOUGLASSII*

		COLOR			SPECTRA (nanometers)			
Spot No.	Race	UV	UV+NH_3	Bene-dicts	METOH	NaOAc	NaOH	$AlCl_2$
1	C.d. – A	D	YG – G	? *	257,264s,327s,367	257,264s,327s,367	267s,330s,424	
	C.b. – A	D	YG – G	? *	254,264s,324,367	254s,264s,329s,368	269,355,449	
	C.b. – B	D	YG – G	? *	250,267s,325,371	245,267s,331s,370	264s,348s,352s,412	
2	C.d. – A	D	YG – G	D *	248,280s,393,365	246,280s,301	246,281,292,330	247,295,324,344
	C.b. – A	D	YG – G	D				
2	C.b. – B	D	YG – G	D				
3	C.d. – A	D	YG	L	266,330s,349	267,352,402s	275,273s,343s,393	276,296s,345,394
	C.b. – A	D	YG	L	266,330s,349	267,352,402s	275,273s,343s,393	276,296s,345,394
3	C.b. – B	D	YG	L				
4	C.d. – A							
4	C.b. – A	D	YG	L	266,330s,349	267,352,402s	275,273s,343s,393	276,296s,345,394
4	C.b. – B	D	YG	L				
5	C.b. – B	d	yg	D				
6	C.b. – B	d	yg	D				
7	C.d. – A	d	y	L				
8	C.d. – A	D	YG	L	267,330s,349	267,352,403s	275,273s,343s,392	276,297s,345,394
	C.b. – A	D	YG	L	267,330s,349	267,352,402s	276,273s,342s,393	276,297s,345,392
	C.b. – B	D	YG	L				
9	C.d. – A	d	y	D				
	C.b. – B							

10	C.b. – C	(D)	YG – G	D	257,303s,360	272,327s,375	272,328s,410	273,297s,368s,413
11	C.b. – C	D	y	D	256,307s,340	257,266s,332	272,400	269,305s,334
12	C.b. – C	D	YG	D				
13	C.b. – C	D	YG	D	256,270s,302s,334	275,327,385	270,389	
14	C.b. – C	D	y	D				
15	C.b. – C	D	YG – G	? *	262s,290,367	232,290	237,322	273,301s,330,409
16	C.b. – C	D	YG – G	D *	267,295s,325s,367			
17	C.b. – C	D	YG	D	257,274s,301s,361	274,324s,385	273,331s,414	274,299s,363s,416
18	C.b. – C	D	y	D				

* Spectra are of aglycones; all others are glycosides.

RACE	C.d. – A	*C. douglassii*
	C.b. – A	*C. bulbosa* – Race A
	C.b. – B	*C. bulbosa* – Race B
	C.b. – C	*C. bulbosa* – Race C
UV	(D)	Very dark spot
	D	Dark spot
	d	Faint dark spot
UV + NH_3	YG	Bright yellow green
	yg	Faint yellow green
	G	Bright green
	y	Faint yellow
BENEDICTS	D	Dark in reflected UV light with Benedicts Reagent
	L	Light in reflected UV light with Benedicts Reagent
SPECTRA (nanometers)	s	Shoulder

of these was not attempted because of the few plants available with which to work. The specimens of Race B came from Pulltight Springs, Missouri, at the type locality of *C. bulbosa* f. *fontinalis* Palmer & Steyermark (1938). The plants were found growing almost totally submerged in cold spring water and therefore differ ecologically from all other populations studied.

Within the limits of the flavonoid chemical data available, *Cardamine douglassii* appears to be one of three chemical races of a highly variable species complex. The wide range of flavonoid chromatographic patterns in *C. bulbosa,* with the slight variation of one of these patterns being *C. douglassii,* may be evolutionally significant if one can assume that a highly variable taxon is likely to be more primitive than a less variable one (Davidson & Dunn, 1967). There is a possibility of finding morphological characters or certain ecologic factors associated with the different chromatographic patterns. This will be discussed further in the section on morphology. The geographic distribution of the chemical races and the possible reasons for this distribution needs further study.

CHROMOSOME NUMBERS

The base chromosome number for *Cardamine* has been reported to be both seven and eight by Lövkvist (1956) in his investigation of the high polyploid *C. pratensis* (Eucardamine) complex. Lewis *et al.* (1962) reported a chromosome number of $n = 32$ in *C. bulbosa* from Texas (base number $= 8$). Haploid counts of $n = 28$ and $n = 56$ (base number $= 7$) have also been reported (Easterly, 1963) from both *C. douglassii* and *C. bulbosa* in a population of plants near Bowling Green, Ohio. In an effort to resolve the conflict in the reported chromosome number for *Cardamine douglassii* and *C. bulbosa,* a cytological investigation was made of several populations of these taxa (Table 3).

Young flower buds were killed and fixed in Carnoy's solution. Snow's acid carmine method was used to stain the meiotic material which was squashed and subsequently

TABLE 3. SUMMARY OF HAPLOID CHROMOSOME NUMBERS AND PERCENT OF POLLEN STAINABILITY WITHIN *CARDAMINE BULBOSA* AND *C. DOUGLASSII*

Species	Population Number	No. of Plants	No. of Counts	Haploid Chromosome Number (n)	Pollen Stainability Average/300 Grains
C. bulbosa	8	7	27	32	98.4
C. bulbosa	9	5	13	32	
C. bulbosa	2	1	3	32	64.9
C. bulbosa	12	4	6	32	82.9
		1	2	32	
			1	40	
		1	7	±40	
		2	3	48	
C. bulbosa	1	4	11	48	
C. douglassii	16	2	3	32	72.3
C. douglassii	19	4	7	32	
C. douglassii	14	1	1	±30	
C. douglassii	18	2	3	32	92.1
C. douglassii	13	10	27	48	99.1
		1	2	48	
			1	32	
C. douglassii	15	2	4	72	
		1	3	48	

mounted in Hoyer's medium (Snow, 1963; Beeks, 1955). Since it was not possible to examine and count all the material within the week it was collected, selected samples were stored, either stained or unstained, in a freezer in 70% ethyl alcohol, for future study.

Meiosis occurs in *Cardamine douglassii* between the beginning of December and early March while it does not occur in *C. bulbosa* until late March and April. This appears to be an important species character; however, it is of little use in field or herbarium identification.

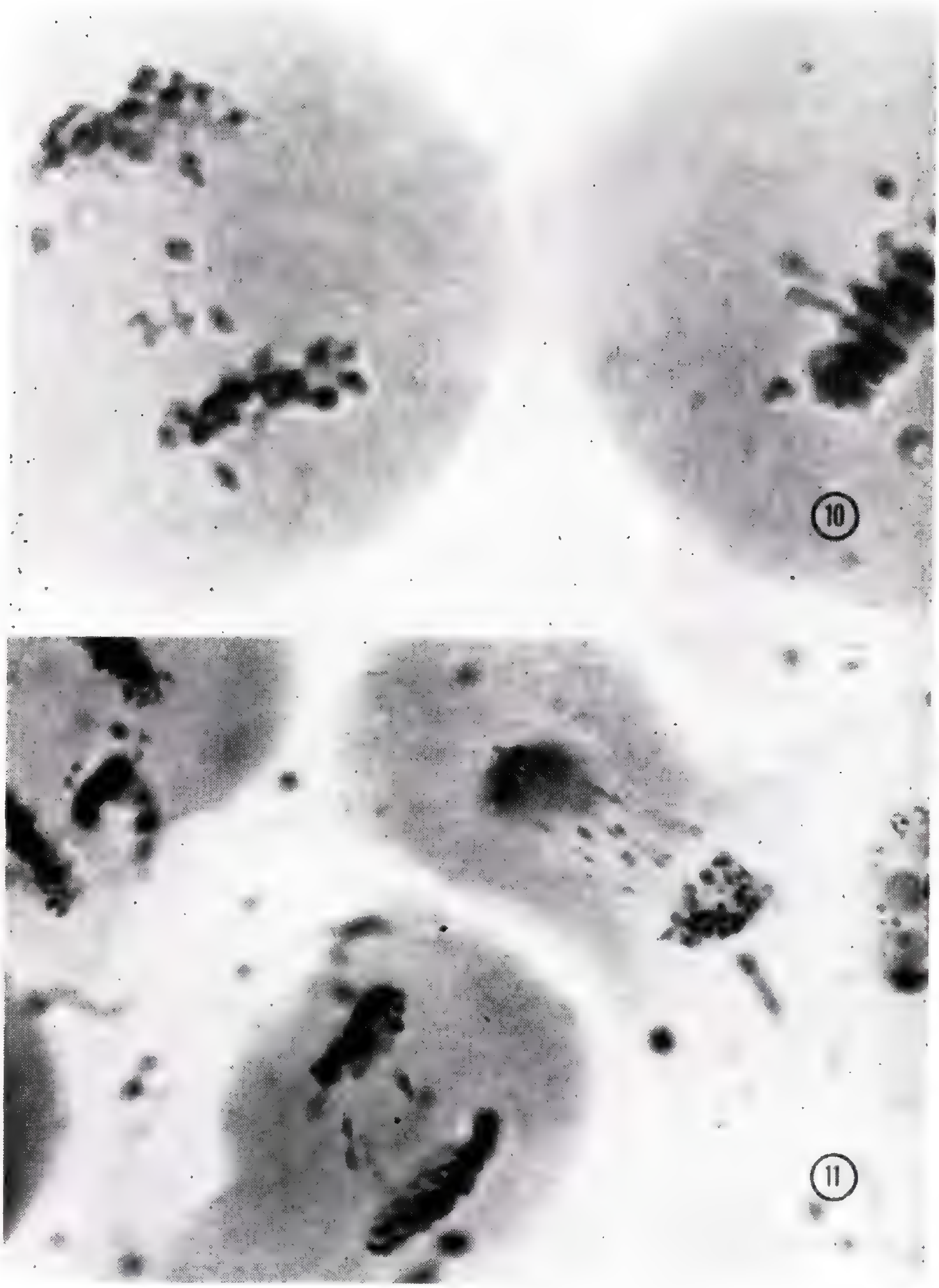
Chromosome counts proved extremely difficult to make as the chromosomes are small and separate with great difficulty. The large majority of plants studied produced no acceptable counts due to either poor separation or a lack of meiotic material.

The most common chromosome number in both species is $n = 32$ (Fig. 2-4) which is found in populations in southwestern Ohio. However, some populations of both species are found to contain higher chromosome numbers. *Cardamine bulbosa,* in the Mammoth Cave populations (pop. 1, 10), possesses a haploid number of 48 (Fig. 6). This number is also found in a few plants of *C. bulbosa* in the Bowling Green population (pop. 12).

The chromosome number of the northern Ohio population of *Cardamine douglassii* differs from the more typical number ($n = 32$) found elsewhere. All plants of *C. douglassii* collected at the Bowling Green, Ohio, site have a haploid number of 48 (Fig. 5). It was also noted that *C. douglassii* from this site produced fewer seeds than produced by this species elsewhere. Plants from this population show a relatively low percentage of good crosses under greenhouse control. These two conditions may be indicative of irregular meiosis in individuals of this population. In Bedford, Ohio (pop. 15), only three plants were counted, two of which have a haploid number of 72 (Fig. 7) and the other, a haploid number of 48 (Table 3).

Two artificially produced F_1 plants (Fig. 8 and 9) resulting from a *Cardamine douglassii* ($n = 32$) × *C. bulbosa* ($n = 32$) cross have meiotic figures with a few lagging chromosomes and possibly incomplete pairing (Fig. 10) with a haploid number near 32. A similar situation was found in a greenhouse hybrid between *C. douglassii* ($n =$

Figs. 2-9. Meiotic chromosomes of *Cardamine bulbosa* and *C. douglassii.* × 1000. Fig. 2. *C. douglassii* from Hueston Woods State Park, Oxford, Ohio ($n = 32$). Fig. 3. *C. douglassii* from John Bachelor Preserve, Oxford, Ohio ($n = 32$). Fig. 4. *C. bulbosa* from Spring Valley, Ohio ($n = 32$). Fig. 5. *C. douglassii* from Bowling Green, Ohio ($n = 48$). Fig. 6. *C. bulbosa* from Three Springs, Mammoth Cave, Kentucky ($n = 48$). Fig. 7. *C. douglassii* from Cleveland Metropolitan Park, Bedford, Ohio ($n = 72$). Fig. 8. Chromosome pattern of hybrid *C. douglassii* ($n = 32$) × *C. bulbosa* ($n = 32$), ($n =$ ca. 32). Fig. 9. Chromosome number of hybrid *C. douglassii* ($n = 32$) × *C. bulbosa* ($n = 32$), ($n =$ ca. $32 + 2$).



Figs. 10-11. Fig. 10. Meiosis in a hybrid, *C. bulbosa* ($n = 32$) × *C. douglassii* ($n = 48$), see text for explanation. Fig. 11. Meiosis in *C. douglassii*, Bowling Green, Ohio ($n = 48$).

48) × *C. bulbosa* ($n = 32$). Lagging chromosomes are common in the buds collected from many plants in different populations (Fig. 11). One putative hybrid collected from the Bowling Green population has a haploid number of ca. 40.

A number of plausible mechanisms could be offered here to explain the presence of the chromosome numbers $n = 48$, $n = 72$ and $n = 40$. However, a more extensive cytological investigation of more individuals and populations will have to be made before any one hypothesis can be advanced over another.

EXPERIMENTAL HYBRIDIZATIONS

The artificial pollinations and hybridizations reported here represent a breeding study undertaken to explore the importance and mechanism of genetic isolation between *Cardamine douglassii* and *C. bulbosa.* The breeding program was undertaken under uniform greenhouse conditions during two growing seasons. Reciprocal crosses between a number of populations of these two taxa were attempted and where possible each cross was undertaken several to many times. Effective emasculation prior to crossing required the removal of the androecium as well as the calyx and corolla. Pollen was transferred to a stigma directly from the anther of the male parent. Initially, the artificially crossed flowers were bagged in glassine envelopes (Kondra & Douney, 1968). However, bagging was discontinued since the self incompatible plants exhibited no outcrossing effects and failed to set seed under normal greenhouse conditions.

Crosses between populations of *Cardamine douglassii* with a haploid chromosome number of 32 show a high percentage of fruit set (85.7%) while crosses between $n = 48$ populations give a low (14.7%) percentage of fruit set. When crosses are made between populations of these two different chromosomal levels the percentage of fruit set is 46.3% when the $n = 32$ individuals are the female parent (Table 4).

TABLE 4. CROSSING RELATIONSHIPS BETWEEN SPECIES AND RACES OF *CARDAMINE BULBOSA* (B) AND *C. DOUGLASSII* (D)

Female	Male	No. of Attempts	No. of Fruits	Percent Fruit Set	Aver. No. seeds/fruit
B(race A) ×	B(race A)	11	11	100	7.2
B(race C) ×	B(race C)	51	40	78.4	5.3
B(BG) ×	B(race A)	23	17	73.9	2.8
B(race A) ×	B(race C)	10	5	50	4.2
B(race A) ×	B(BG)	3	0	0	—
B(race A) ×	B (n = 48)	1	1	100	1
B(n = 48) ×	B(race C)	2	0	0	—
B(n = 48) ×	B(BG)	3	0	0	—
B(BG) ×	B(n = 48)	2	2	100	3
B(n = 48) ×	D(n = 48)	4	0	0	—
B(race A) ×	D(n = 32)	28	10	57.1	3.3
B(race C) ×	D(n = 32)	110	31	32.7	5.9
B(race C) ×	D(n = 48)	23	19	82.6	5.6
B(BG) ×	D(n = 32)	23	11	60.9	2.6
B(BG) ×	D(n = 48)	3	2	66.7	2.5
D(n = 32) ×	D(n = 32)	14	12	85.7	5.3
D(n = 48) ×	D(n = 48)	14	2	14.3	5.0
D(n = 32) ×	D(n = 48)	41	19	46.3	5.8
D(n = 48) ×	D(n = 32)	25	7	28	4.9
D(n = 32) ×	B(race A)	24	15	62.5	8.6
D(n = 32) ×	B(race C)	59	18	30.5	7.8
D(n = 48) ×	B(race C)	19	0	0	—
D(n = 48) ×	B(BG)	5	3	60	5.3
B(race A)	Selfed	9	0	0	—
B(race C)	Selfed	8	0	0	—
D(n = 32)	Selfed	26	1	3.8	1
D(n = 48)	Selfed	16	1	6.3	1

With the exception of the Bowling Green *Cardamine bulbosa*, Bowling Green *C. douglassii* is generally isolated from the other races when used as a female parent. Interestingly, when *C. douglassii* ($n = 48$) pollen is put on the stigma of *C. bulbosa* (chemical Race C) fruit set is 82.6 percent while in the same cross with other chemical races there is no fruit set.

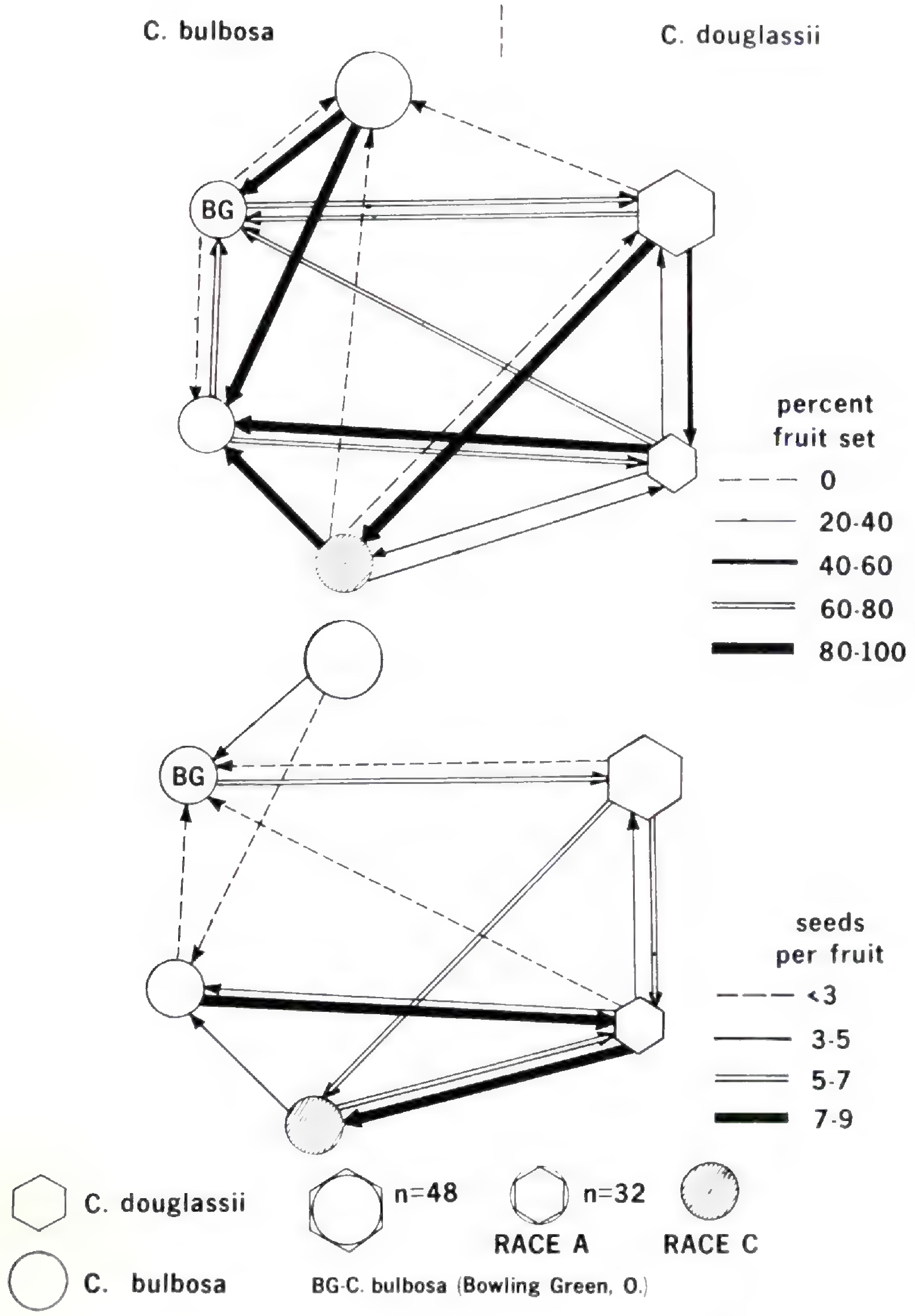


Fig. 12. Percentage of fruit set and number of seeds per fruit in intraspecific and interspecific crosses of *C. bulbosa* and *C. douglassii.*

One should note that although only a few crosses could be made, the preliminary evidence indicates that the *Cardamine bulbosa* ($n = 32$) of the Bowling Green population may act as a good female parent for all races tested, including those with a haploid number of 48 (Fig. 12). While many fruits are produced on these plants, there appears to be a decrease in the number of seeds per fruit (Table 4, Fig. 12).

Since putative hybrids have been found in the field, it is desirable to know the fertility of artificially produced, greenhouse grown hybrids for comparison with their parents. Crosses of hybrids $F_1 \times F_1$ produce fruit from 30 percent of the attempts. Of the eight F_2 plants grown to flowering size, only three actually flowered. This was unusual as all other plants raised in this study flowered with little difficulty when mature and after being vernalized at 4° C. for two months. This F_2 breakdown did not seem to affect those plants which did flower, as eight good fruits with an average of four seeds each were produced from eight attempted crosses with other F_2's (Table 5).

Backcrosses of *Cardamine douglassii* ($n = 32$) and *C. bulbosa* (chemical Race A) to the F_1's were easily made as was the reciprocal to *C. bulbosa* (Table 5). The relative ease in making backcrosses indicates that a large amount of gene flow between the two species is possible.

The chromosome race of *C. bulbosa* ($n = 48$) found in Kentucky was not studied in detail; however, from a total of fourteen crosses attempted (Table 4) it appears as though the race may behave somewhat like the Bowling Green population of *Cardamine douglassii* ($n = 48$). *Cardamine bulbosa,* having a haploid number of forty-eight, may act as the female parent only with difficulty while it serves as the male parent with ease (Fig. 12). Only four crosses of the Kentucky *C. bulbosa* ($n = 48$) and *C. douglassii* ($n = 48$) were tried, and none produced fruit.

Preliminary work demonstrates that both species of *Cardamine* are protogynous. The stigma often emerges one or two days before the flower opens and two to three

TABLE 5. CROSSING RELATIONSHIPS OF THE HYBRIDS OF *CARDAMINE BULBOSA* AND *C. DOUGLASSII*

Female	Male	No. Attempts	No. Fruit	Percent Fruit set	Average No. Seeds/Fruit
F_1 (n = 32, race A) ×	F_1 (n = 32, race A)	153	56	36.6	7.1
F_1 (n = 32, race C) ×	F_1 (n = 32, race A)	50	3	6.0	3.0
F_1 (n = 32, race A) ×	F_1 (n = 48, race A)	8	5	62.5	1.2
F_1 selfed		20	0	0	—
F_1 (n = 32, race A) ×	B (race C)	4	1	25	5
F_1 (n = 32, race A) ×	B (race A)	12	12	100	8.9
F_1 (n = 32, race A) ×	D (n = 32)	45	30	66.7	11.07
B (race A) ×	F_1 (n = 32, race A)	31	31	100	7.5
B (race C) ×	F_1 (n = 32, race A)	4	2	50	6.0
D (n = 32) ×	F_1 (n = 32, race A)	12	2	16.7	5
F_2 ×	F_2	8	8	100	4.0
F_1 (n = 32, race A) ×	F_2	4	1	25	4.0

B = *C. bulbosa*
D = *C. douglassii*
F_1 = *C. bulbosa* crossed with *C. douglassii*
F_2 = F_1 crossed with F_1
n = 32 *C. douglassii* (n = 32)
n = 48 *C. douglassii* (n = 32)

race A — *C. bulbosa* (chemical race A)
race C — *C. bulbosa* (chemical race C)

Fig. 13. *C. bulbosa* with the stigma protruding prior to anthesis, suggesting incipient protogyny.

days before the anthers dehisce (Fig. 13). Tests have shown the stigma to be receptive at this time. Protogyny has been reported in the Cruciferae and related genera before (Harriman, 1965; Johnson, 1971; Rollins, 1971).

An examination of the crossing relationships of *Cardamine douglassii* and *C. bulbosa* has revealed some interesting facts. As previously mentioned, *C. bulbosa* appears to be composed of at least three chemical races; however, while both races A and C cross among themselves and produce fruit almost 80 percent of the time (Table 4), their crossability to *C. douglassii* differs. *Cardamine bulbosa* (chemical Race A) produces fruit about 60 percent of the time when it is crossed to *C. douglassii* ($n = 32$) while *C. bulbosa* (chemical Race C) produces fruit only a little over 30 percent of the time. When fruits are produced, little difference is noted in seed production in crosses between the two chemical races and *C. douglassii*. The ability of the Race C to cross with the F_1's of the aforementioned cross is distinctly less than that of Race A.

Crossing relationships indicate possible genetic differences between the chemical races of *Cardamine bulbosa.* Chemical Race C seems slightly more isolated from *C. douglassii* than does the chemical Race A as far as the production of F_1's and backcrosses is concerned. It is possible that Race C is a later adaptation of *C. bulbosa,* less apt to hybridize with *C. douglassii.* Another possibility is that *C. bulbosa* (Race A) is a variant originating from hybridization and later backcrossing between *C. bulbosa* (Race C) and *C. douglassii.* Its geographic distribution needs further study in light of this possibility.

The chromosome race $n = 48$ of *Cardamine douglassii* has a lower fruit set than the other populations when intrapopulational crosses are made (Table 4). Data from crosses between populations having different chromosome numbers (at least in *C. douglassii*) indicate the isolation of these populations from each other. *Cardamine douglassii* ($n = 48$) does not act as a good female parent in interspecific crosses. The fact that one population of *C. bulbosa* which is sympatric with a *C. douglassii* ($n = 48$) population can cross readily with it indicates a breakdown of what genetic isolation mechanisms there are in this population. One might expect that in the Bowling Green, Ohio, population, where *C. bulbosa* ($n = 32$) and *C. douglassii* ($n = 48$) are capable of hybridizing, there would be hybrids present as well as the possibility of many backcrossed plants.

Interspecific crosses proved relatively easy to make, at least as easy as some interracial crosses within species. This indicates that genetic incompatibility is not an important isolating mechanism separating *Cardamine bulbosa* and *C. douglassii* except where different chromosome numbers exist. All artificial crosses were made in the greenhouse at Miami University. In the field, examination of putative hybrids showed that there is some fruit development but that very few seeds mature.

When hybrid crosses are made in nature, during the slight overlap in blooming time, it is most likely that the

Cardamine douglassii pollen would be transferred to the emergent stigma of *C. bulbosa.* At the time of overlap, *C. bulbosa* is just beginning to flower while *C. douglassii* flowers are wide open. Because of protogyny, the flowers of *C. douglassii* would be pollinated with *C. douglassii* pollen by this time. If pollinator inconsistency is assumed, an interspecific cross with *C. bulbosa* as the female parent would be more likely than the reverse.

Only a small difference in number of fruits set is noticed between *Cardamine bulbosa* (Chemical Race A, $n = 32$) and *C. douglassii.* Important differences, however, can be seen in number of seeds per fruit (Fig. 12). The more easily accomplished cross using *C. bulbosa* as female parent produces fruit with a few seeds while the more difficult cross using *C. douglassii* as female parent leads to the production of fruit with many seeds.

At first glance, the phenomenon of protogyny in these self incompatible species is perplexing as it cannot increase outcrossing, although it may prevent a wastage of gametes. It appears that in these two closely related *Cardamine* species protogyny is at least partially responsible for keeping these species evolutionarily separate. Johnson (1970) may have found a similar situation in *Arabis holboellii* and the closely related *A. sparsiflora.*

PHENOLOGY

Since the two species are supposedly isolated due to different flowering times, the flowering period of *Cardamine bulbosa* and *C. douglassii* was studied over two growing seasons. Starting in late March through early June, two to three visits a week were made to four different areas in southwestern Ohio. Each of these sites contained both *C. bulbosa* and *C. douglassii.* Two quadrats (ca. 10′ × 10′) were established at each site and the number of plants of each species in bloom at each visit was noted.

Phenology of *Cardamine bulbosa* and *C. douglassii* is shown for the spring seasons of 1969 and 1970 (Fig. 14).

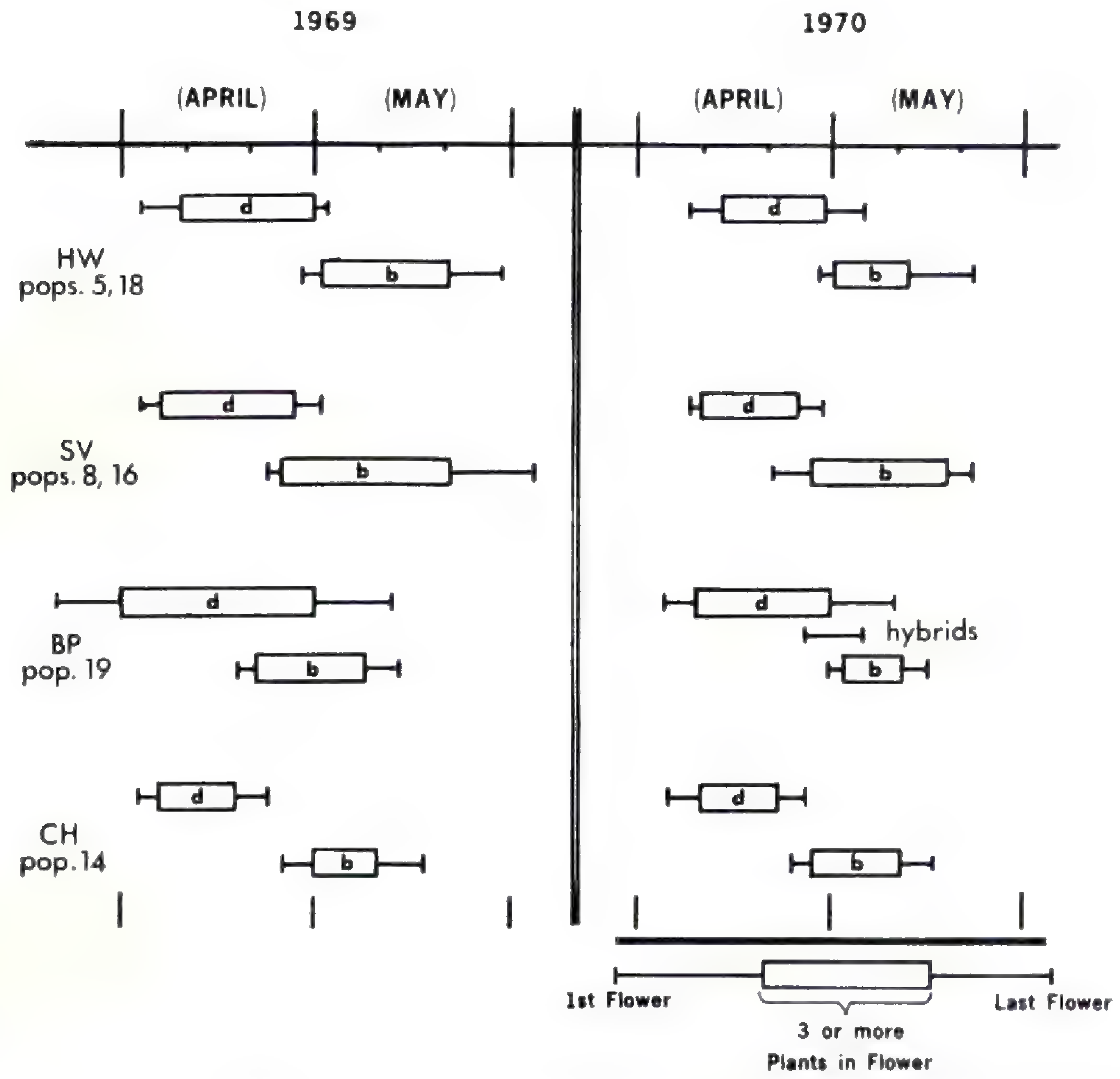


Fig. 14. Time of flowering sequence of *Cardamine douglassii* (d) and *C. bulbosa* (b) in southwestern Ohio. 100 sq. ft. quadrat.

Each rectangle in Figure 14 indicates the period of time three or more plants were in bloom in that particular quadrat. The horizontal line extending in either direction indicates the time the first and last plant of that species was in bloom in the neighboring area. *Cardamine douglassii* begins flowering around the first week of April and continues until early May. *Cardamine bulbosa,* on the other hand, begins flowering around the last week of April and may continue into June.

While these two species flower at largely different times, an overlap of flowering does occur in late April. Stuckey (1962) noticed a similar situation in Michigan. However,

due to the more northern position of that state, the overlap period occurred in mid-May. Putative hybrids (based on intermediate pubescence length and height) have been found at the phenological site on the John Bachelor Preserve near Oxford, Ohio. Putative hybrid plants at this and other locations have an intermediate flowering time between the parental types.

While *Cardamine bulbosa* and *C. douglassii* flower at different times, the overlap is such that one might expect hybrids to be produced relatively often. The overlap does vary from year to year and from site to site ranging from almost complete overlap at the John Bachelor Preserve near Oxford, Ohio, in 1969 (population no. 19), to no overlap at all at Camp Hook (Boy Scout camp) near Franklin, Ohio (population no. 14), in the same year.

POLLINATION

Hybridization in nature is mediated through the activities of pollinators. One bee visiting different species of *Cardamine* could possibly cause interspecific hybridization. In an attempt to identify the visiting insects, hopefully the pollinators, those insects visiting either *C. bulbosa* or *C. douglassii* were collected during the spring of 1969 and 1970. Collections were made on clear days since cloudy days produced little pollinator activity. Insects were netted between ten in the morning and three in the afternoon. An attempt was made to collect nearly all insects seen without creating a disturbance which might frighten certain species away. *Apis mellifera* may be over-represented due to its size. However, this was realized at the time of collection.

Pollen from the corbicular load was removed and mounted in Hoyer's solution stained with fast green. It is not easy to distinguish the pollen of the different genera of the Cruciferae, let alone separate *Cardamine bulbosa* pollen from that of *C. douglassii.* It is believed that relative abundance of crucifer pollen grains (out of sample of 300 grains) contained in the corbicular load of a bee can be

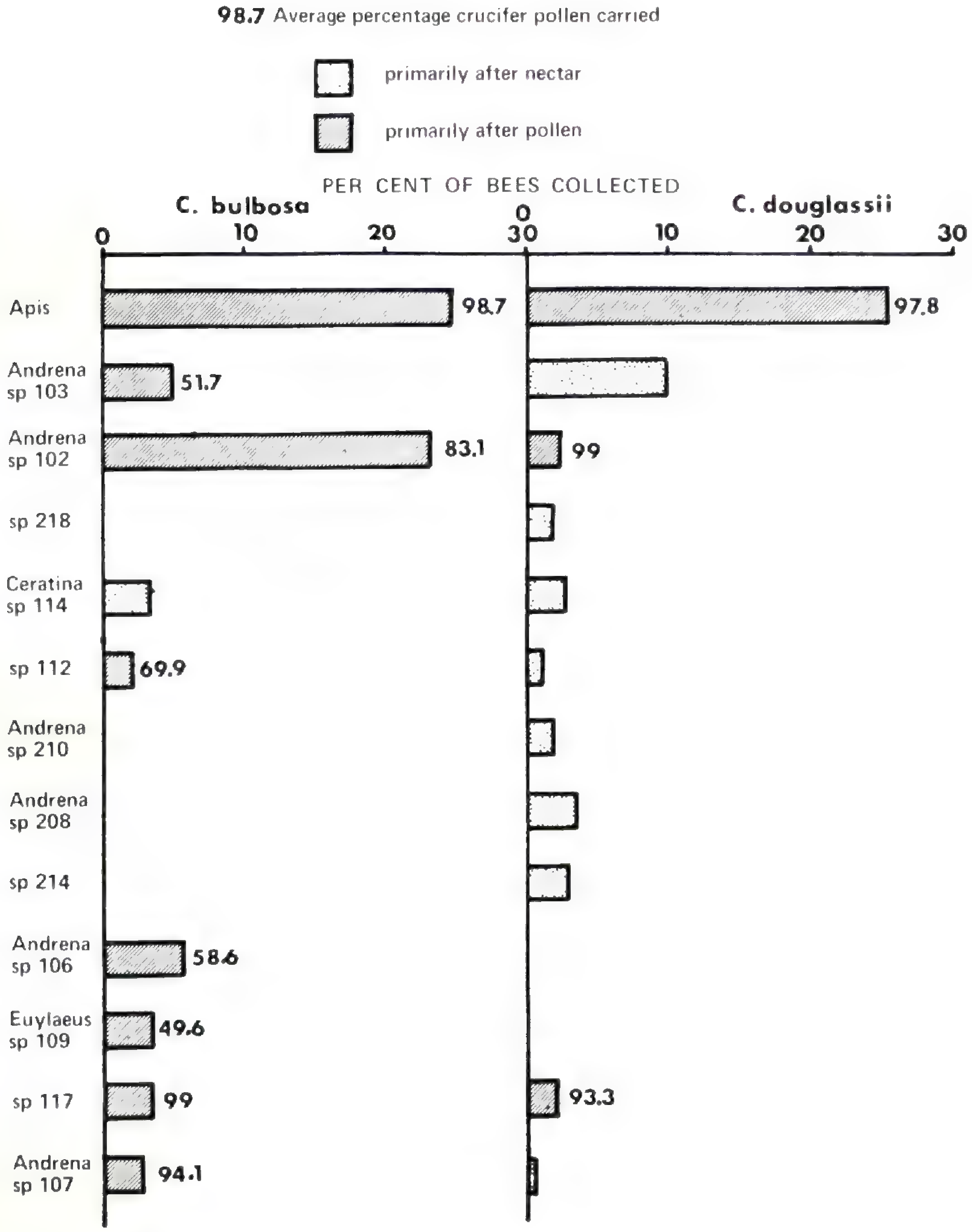


Fig. 15. Visitors to *Cardamine douglassii* and *C. bulbosa* including the percentage of Crucifer pollen carried in their corbicular loads.

used as an indication of the constancy that the bee exhibited for Cruciferae and possibly for the particular crucifer on which it was collected. Bees were identified to genus by using Mitchell's (1960, 1962) keys. Species identification was not attempted in most cases. The specimens have been sent to Dr. R. Fisher at Michigan State University for further verification.

One hundred and forty-three insects were taken visiting *Cardamine bulbosa* and two hundred and fifty-nine visiting *C. douglassii.* The most common bee collected on both species was *Apis mellifera* (Fig. 15). Robertson (1928) did not report honey bees as visitors of *C. bulbosa.* Although honey bees are apparently lacking from many *C. bulbosa* communities, we found that they are active visitors in some. One member of the genus *Andrena* (sp. 102) is very common on *C. bulbosa.* This species, while sometimes found on *C. douglassii,* is of secondary importance on this earlier flowering species.

Apis mellifera is by far the most common visitor of *Cardamine douglassii* (Fig. 16). Another species of *Andrena* (sp. 103) makes about ten percent of the visits to *Cardamine douglassii* and is primarily a nectar feeder. This species is probably not as important a pollinator as its numbers indicate since its method of collecting nectar frequently entails getting it from the outside of the flower (Fig. 17). Near the end of the flowering season of *C. douglassii, Andrena* (sp. 103) began to collect some pollen. This species, therefore, is of more importance later in the season as a pollinator of both species and possibly between the two species.

Apis mellifera is quite constant as to the pollen it collects (Fig. 15). The smaller bees are noticeably less specific as to the plants they visit. This has been reported numerous times before (Grant, 1950). It was further noticed that with the exception of *Apis mellifera,* which collects both nectar and pollen, the visitors to *C. douglassii* are most often after nectar while those of *C. bulbosa* are pollen gatherers.

Figs. 16-17. Fig. 16. *Apis mellifera* foraging on *Cardamine douglassii.* Fig. 17. *Andrena* sp. (sp 103) visiting *C. douglassii.*

The insect species most likely to visit the flowers of both species as far as numbers are concerned appears to be *Apis mellifera*. However, it seems quite species-specific at any one time. This, of course, may not be true with the new bees fresh from the hive (Grant, 1950; Butler, 1945). The two common species of *Andrena* (nos. 102, 103) appear to be less constant as to the flowers they visit and therefore more likely to act as cross pollinators of the two species.

ECOLOGY

Stuckey (1962) and others previously proposed ecological factors as possible isolating mechanisms between the two taxa under investigation. To test this hypothesis twenty-three communities in which one or both of the *Cardamine* species were found (Table 1, 6) were studied. Three transects six feet wide and a minimum of 300 feet long were made through each community in which the species were growing. All of the woody plant species present within the transects were recorded, including their diameter at breast height (DBH). Seedling trees were considered to have a DBH of less than one inch, while sapling trees had a DBH of 1-6 inches and canopy trees had a DBH greater than six inches. This method allowed the calculation of abundance and basal area but did not allow calculation of frequency.

Estimates of species composition and abundance of herbaceous flora within a community were made by sampling five or more one meter square quadrats at random. After visual estimates of the abundance of the various species had been made, they were classified into three categories: abundant (3), common (2), rare (1). Plants present in the community but not located within one of the five quadrats were also noted. Community abundance of the herbaceous species was projected by summing the abundant (3), common (2), or rare (1) values of each species for the five quadrats. In this system a species that was abundant in all five herbaceous quadrats would then have an abundance value of 15.

Soil moisture was calculated at intervals throughout the spring and early summer for two years in many of the communities. Soil from the upper four inches was collected into airtight jars, and weighed immediately upon return to the lab. This soil was dried at 105°C for 48 hours and reweighed. The percent water in the soil was then calculated with percentages greater than 100 percent, assumed to be 100 percent.

Importance percentages of the more abundant woody species were calculated by the Jackson and Petty (1971) method. Jackson and Petty argue that weighing the percent basal area (dominance index) twice as much as the density (percent abundance) gives a more ecologically accurate expression of a species' contribution to a community in disturbed old-growth forests.

The importance value, percent water, abundance, basal area, number of canopy trees per acre, and pH were used in a regression with 17 morphological characters to study character relationships (Hart, 1972; Appendix 8).

Similarities between the study areas were tested with the use of a Cluster Program by G. F. Bonham-Carter (1967). This technique used presence-absence data as opposed to Hall's (1970) semiquantitative data method. Jaccard's coefficient (Sokal & Sneath, 1963; Sneath & Sokal, 1973) was also found to be quite useful. This coefficient prevents a high degree of association from occurring between objects lacking a large number of characters in common. Similarity, as expressed by this coefficient, is a measure of the similarity of plants present in the various communities.

The weighted pair group method, using average linkage, was used in clustering the Operational Taxonomic Units (OTU's) of the association coefficient matrix (Sokal & Sneath, 1963; Sneath & Sokal, 1973).

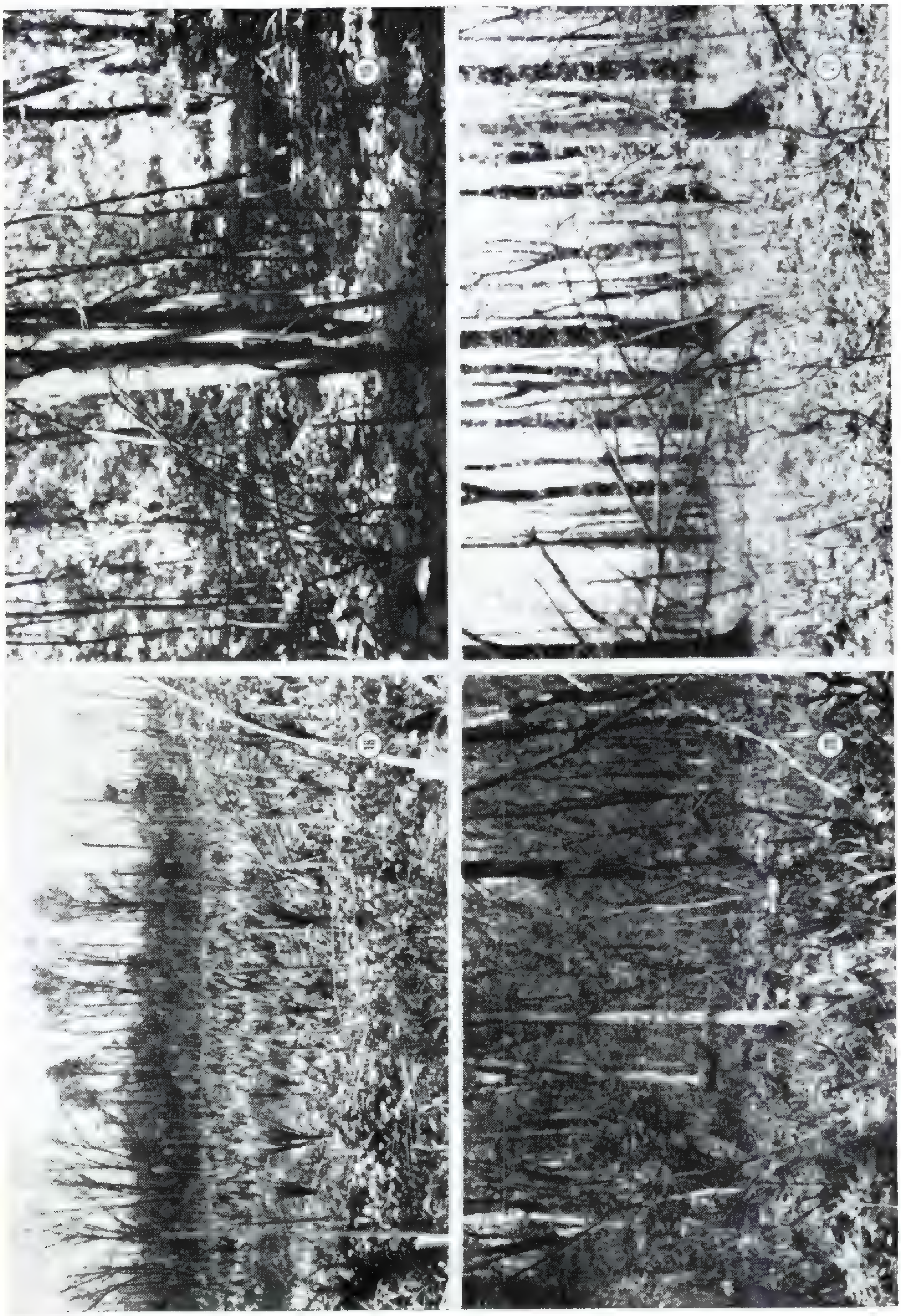
Both the Q-mode or comparison between samples (populations) and the R-mode or comparison between variables (plant species) analyses were used for clustering in this study. The Q-mode association comparing populations is

based on presence and absence data while the R-mode analysis is based on semiquantitative data.

Twenty-three populations containing *Cardamine douglassii* and/or *C. bulbosa* were compared for their herbaceous vegetation. Both Jaccard's coefficient and Sokal and Michner's (Sokal & Sneath, 1963; Sneath & Sokal, 1973) coefficient were used. Of a total of 191 herbaceous species encountered within one or more of the twenty-three populations, only those ninety-seven species present in two or more communities were used. This arbitrary limitation was necessary due to the lack of a computer program capable of handling a matrix including all the species.

Community similarity, based on the presence or absence of all sixty-eight woody species encountered, was computed by both Jaccard's and Sokal and Michner's association coefficient and clustered by both the weighted and unweighted method. Only twenty-two populations were compared as opposed to the twenty-three populations used in comparison of the herbaceous species. This was necessary since there are no woody species in one community studied near Cincinnati, Ohio, which is periodically mowed throughout the summer and fall.

The R-mode approach, which is based on only presence or absence of a species, has been questioned as a statistic by Siegal (1956). For this reason the species comparison has been based on semiquantitative data (Hall, 1970). The community abundance of each species ranges from one through fifteen. This abundance was split into five groups: abundant (11-15), very common (6-10), common (2-5), rare (from present in community but not in a quadrat to a community abundance of one), and absent. This particular breakdown of community abundance values was chosen since it allowed each of the categories to contain a more equal number of species. It was also felt that this would give increased cognizance of the rarer species while decreasing the relative importance of the more common and abundant species.



Figs. 18-21. Fig. 18. *Cardamine bulbosa* community, Spring Valley, Ohio. Fig. 19. *Cardamine bulbosa* community, Cincinnati Country Day School, near Cincinnati, Ohio. Fig. 20. *Cardamine douglassii* community, Bachelor Estate, near Oxford, Ohio. Fig. 21. *Cardamine douglassii* and *C. bulbosa* community, many putative hybrids present, near Bowling Green, Ohio.

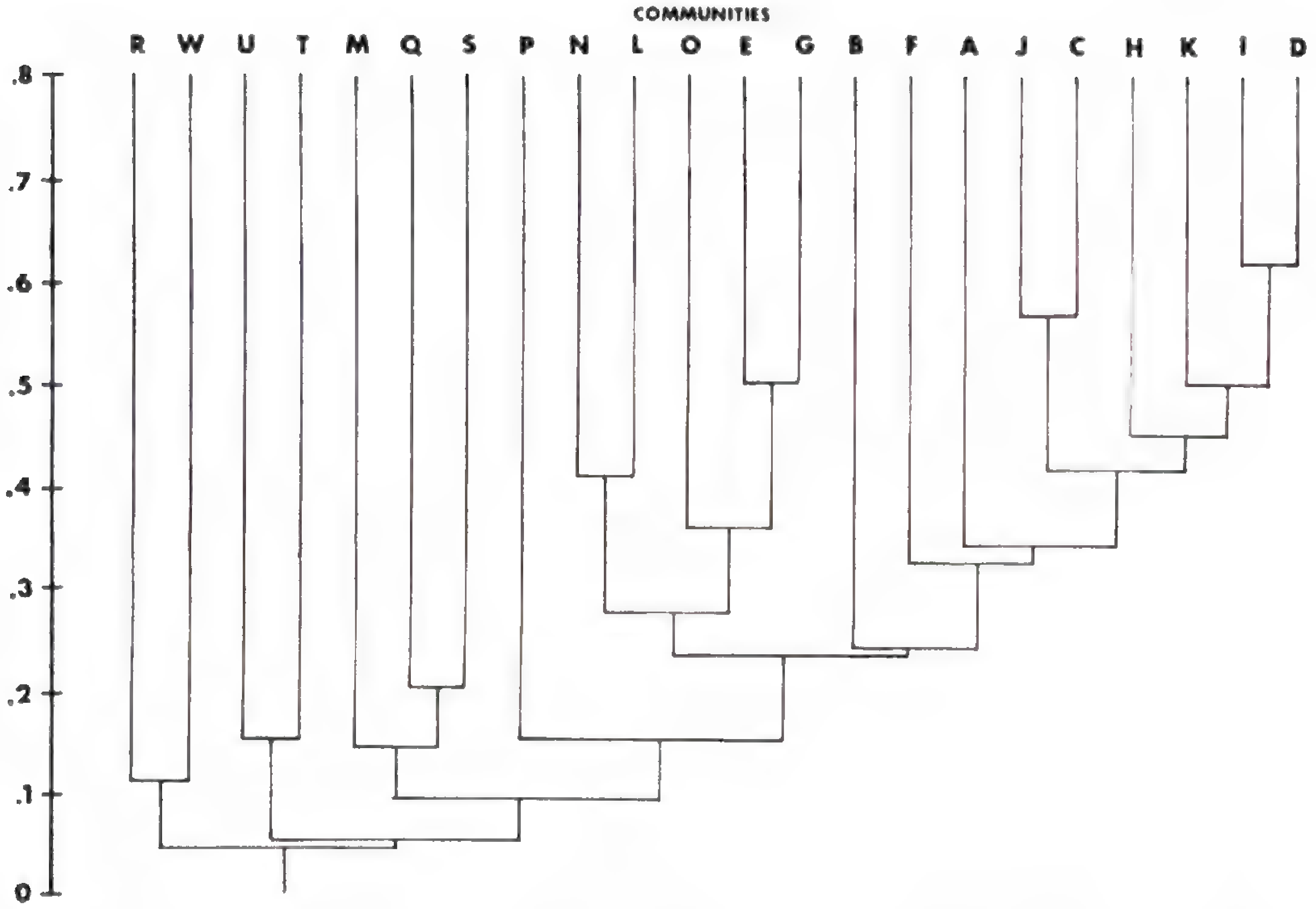


Fig. 22. Population similarity based on the woody species present in the community. Jaccard's coefficient clustered by the weighted pair-group method. Mean expected value = 0.0932.

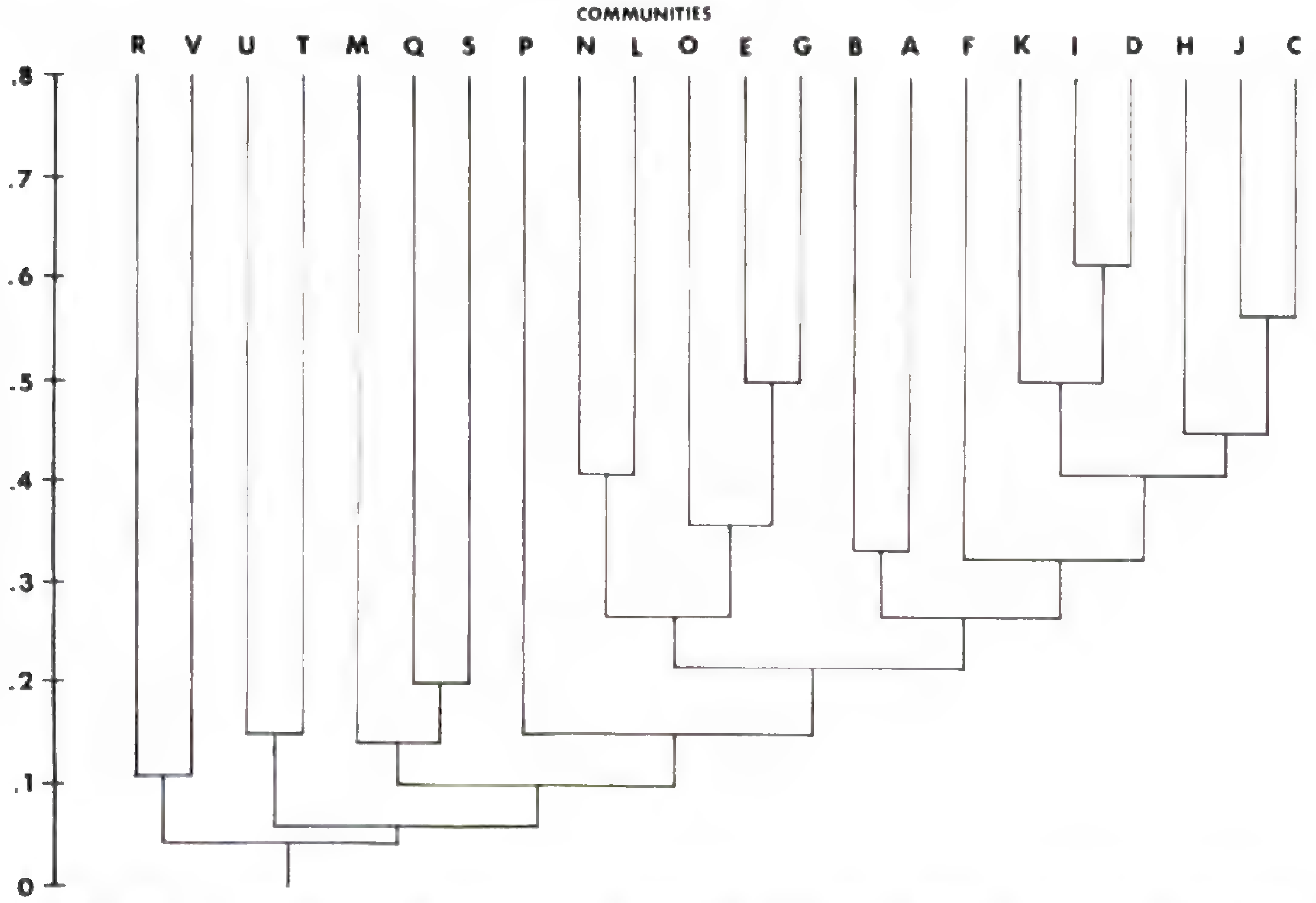


Fig. 23. Population similarity based on the woody species present in the community. Jaccard's coefficient clustered by the unweighted pair-group method. Mean expected value = 0.0932.

The variation of habitats in which the species were found is shown in the four community photographs (Figs. 18-21). Similarity based on the presence of woody species (Jaccard's coefficient) does not reveal a clear cut separation (Fig. 22, 23). However, several interesting associations do occur. The community at Rush Run (Com. G) containing *Cardamine douglassii* is different from the others in southwestern Ohio. It has a strong association (about 0.5) with the northern community in Bedford, Ohio (Com. E). Both communities have relatively high amounts of water in the soil. Both of these communities cluster with three *C. bulbosa* communities, one from the Illinoian till plain of southwestern Ohio (Com. O) and two others from Kentucky (Com. N, L). It is also of interest to note that the woody species on the hillside and the adjacent floodplain at the John Bachelor Preserve (Com. I, J) near Oxford, Ohio, are not very similar as they fail to cluster closely together.

The Sokal and Michner coefficient takes into consideration the absence of a species and causes some noticeable changes in the form of the dendrogram (Fig. 24, 25). For instance, Cedar Swamp, an alkaline bog with northern affinities (Dachnowski, 1910), is shown to be unlike all other communities. The weighted cluster (Fig. 24) shows five major groups. One is the community at Cedar Swamp (Com. T). The second is the two communities studied near Bowling Green, Ohio (Com. B, A), which have both *Cardamine* species and apparent hybrids intermixed. The third group contains a mixture of communities: one *C. douglassii* from southwestern Ohio (Com. G), one *C. douglassii* from northern Ohio (Com. E), one from the Illinoian till plain of southern Ohio (Com. O), and two from Kentucky containing *C. bulbosa* (Com. N, L). The fourth group contains the six remaining communities in which *C. douglassii* (Com. C, D, H, I, J, K) is important. The remaining cluster contains communities which have relatively large numbers of *C. bulbosa,* although one (Com. P) does contain a few *C. douglassii.*

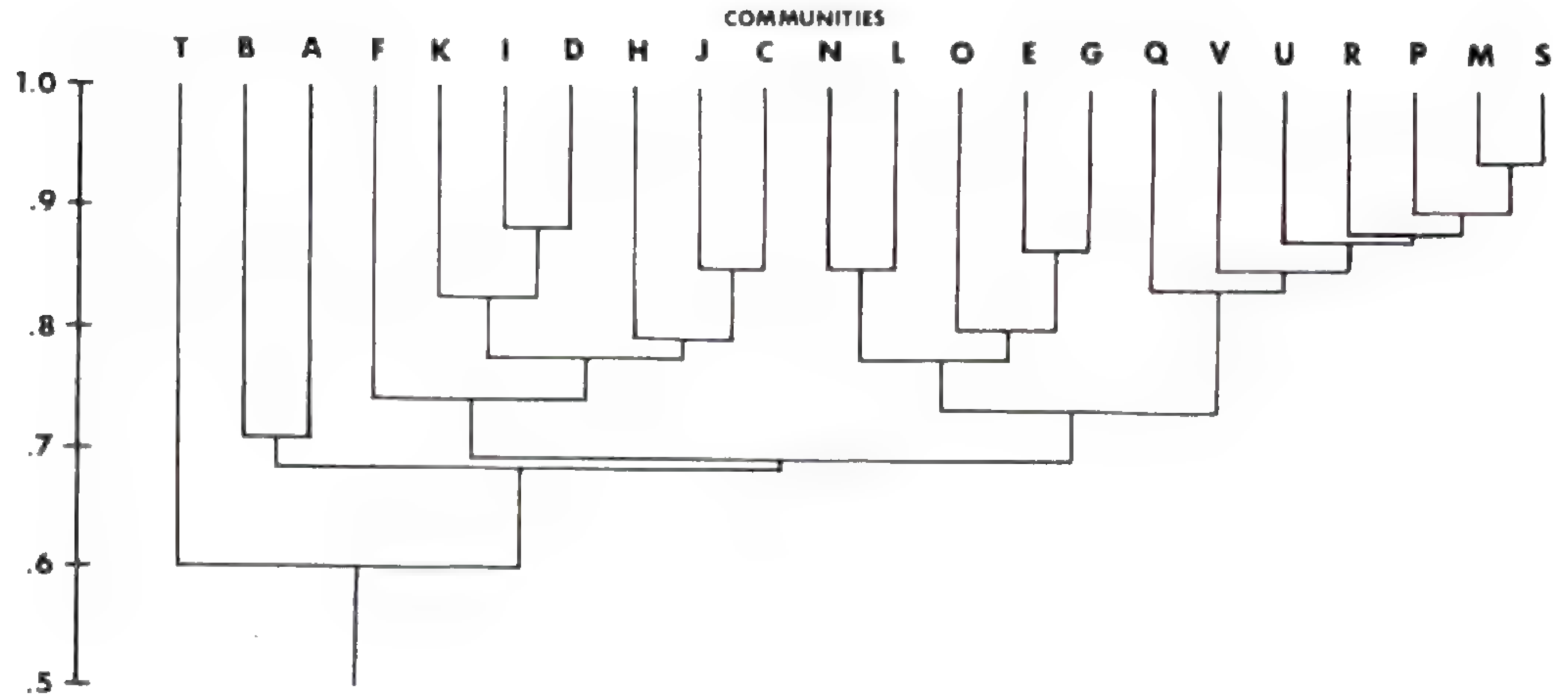


Fig. 24. Population similarity based on the woody species present in the community. Sokal and Michener's coefficient clustered by the weighted pair-group method. Mean expected value = 0.694.

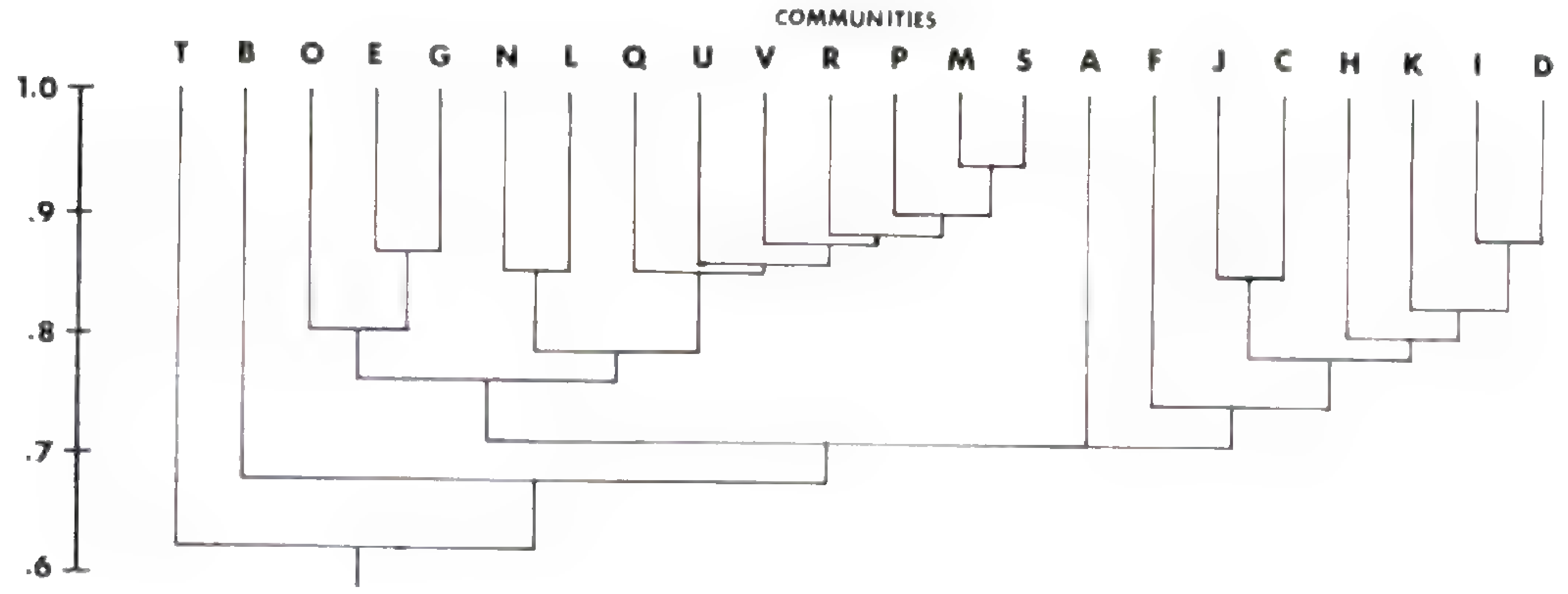


Fig. 25. Population similarity based on the woody species present in the community. Sokal and Michener's coefficient clustered by the unweighted pair-group method. Mean expected value = 0.0694.

The unweighted pair group method (Fig. 25) is basically similar but with the Kentucky communities (Com. L, M, N) and two communities containing *Cardamine douglassii* (Com. E, G) clustering with the communities containing large numbers of *C. bulbosa*. The Cedar Swamp community (Com. T) and one from Bowling Green (Com. B) are somewhat isolated from the others.

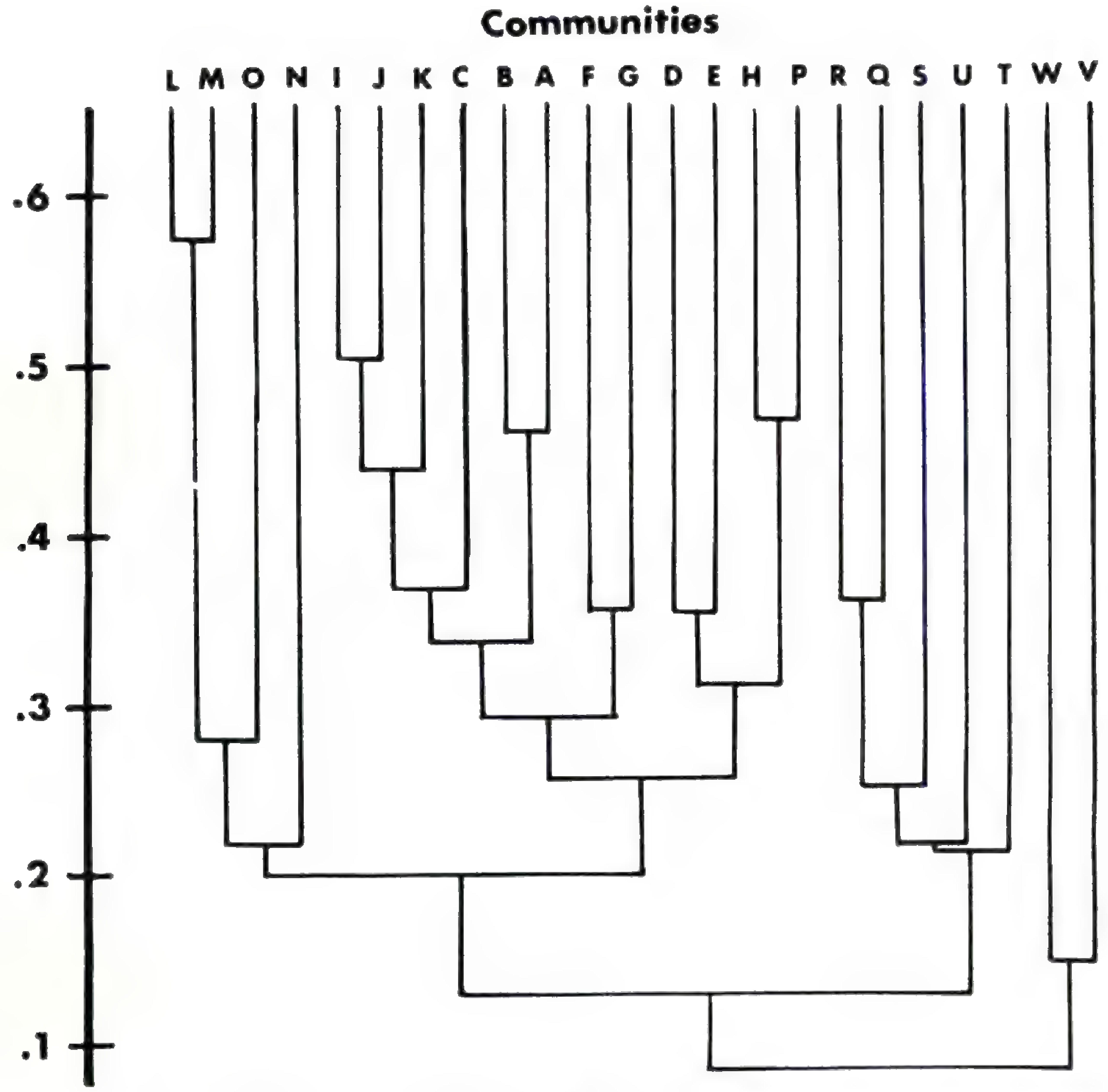


Fig. 26. Population similarity based on the herbaceous species present in the community. Jaccard's coefficient clustered by the weighted pair-group method. Mean expected value = 0.105.

Jaccard's coefficient based on the presence of herbaceous species produces four easily recognizable clusters (Fig. 26, 27). One group (Com. L, M, O, N) contains the communities from the Illinoian till plain east of Cincinnati, Ohio, and from the unglaciated populations of Kentucky. Others containing *Cardamine bulbosa* but not *C. douglassii* (Com. R, Q, S, U, T, V) are high in water except for the unusual community (Com. W) where *C. bulbosa* is found in a mowed field (Table 6). The remaining group is composed of communities where *C. douglassii*, with or without *C. bulbosa*, is found.

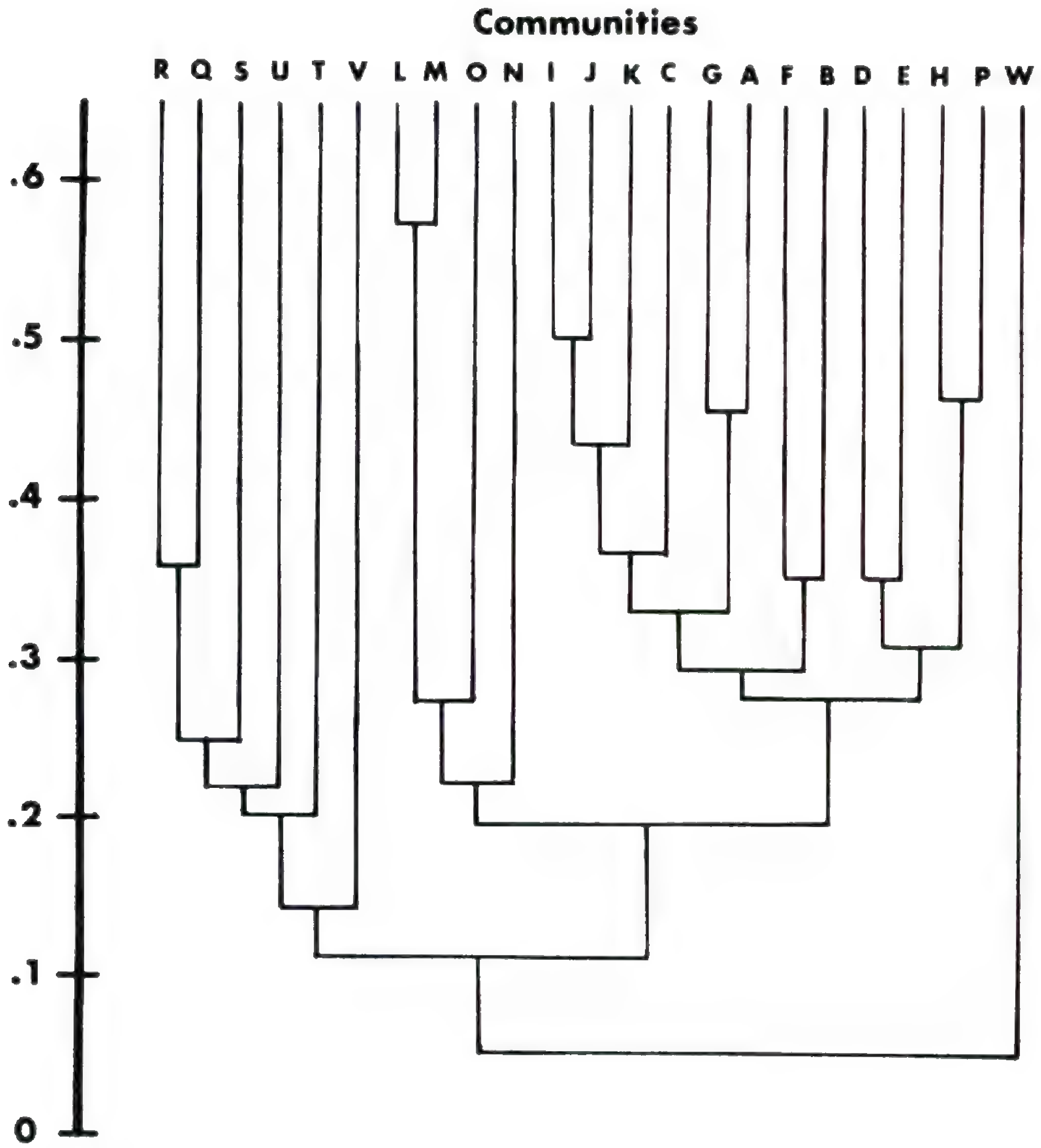


Fig. 27. Population similarity based on the herbaceous species present in the community. Jaccard's coefficient clustered by the unweighted pair-group method. Mean expected value = 0.105.

When considering both presence and absence (Sokal & Michner's coefficient), the unglaciated populations do not form a separate cluster. The weighted pair-group method (Fig. 28) separates the twenty-three communities into two major groups. This division is not related to particular *Cardamine* species but appears to be associated with the number of large woody plants present and the presence of large amounts of water. The communities in the smaller

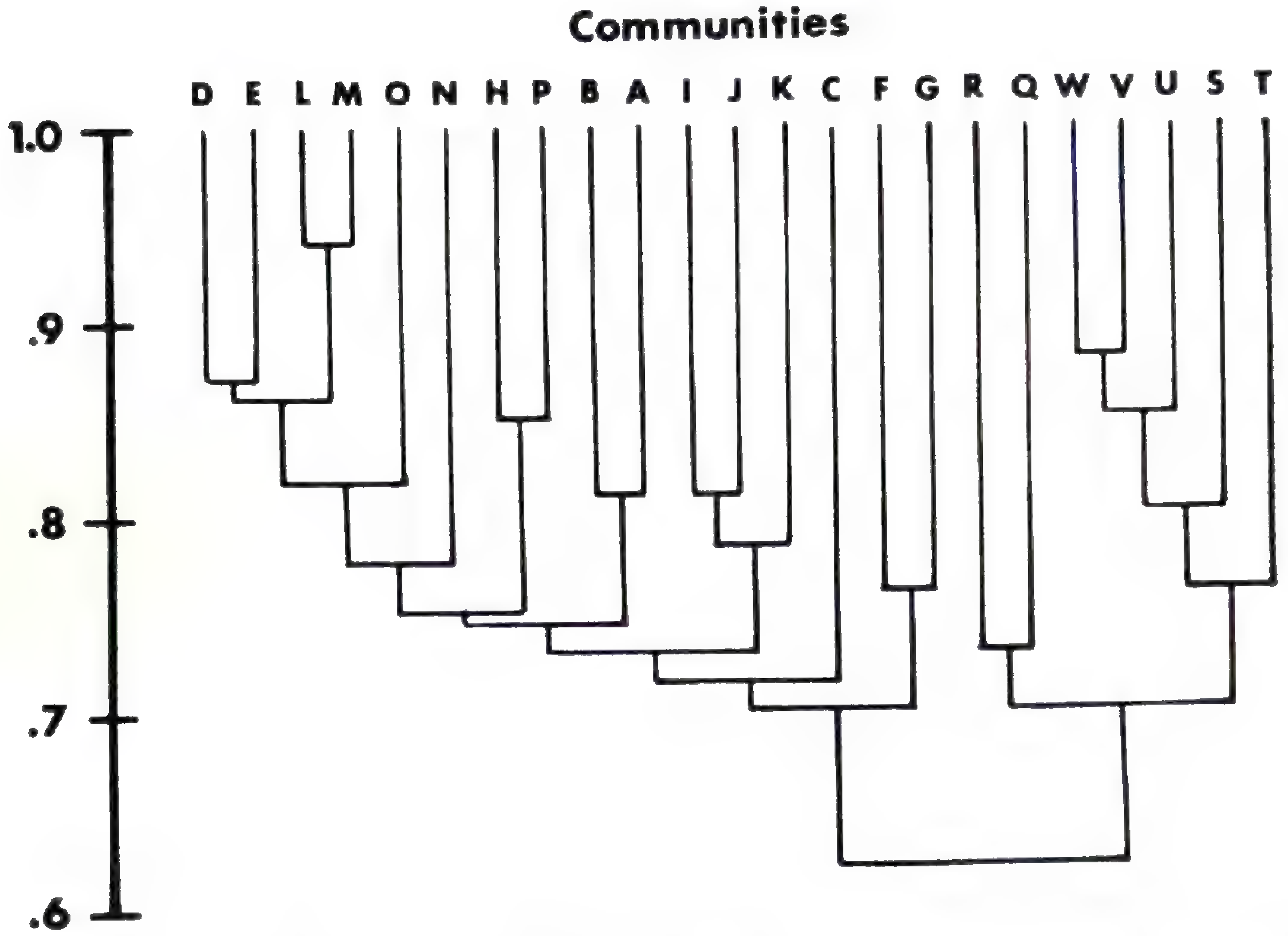


Fig. 28. Population similarity based on the herbaceous species present in the community. Sokal and Michener's coefficient clustered by the weighted pair-group method. Mean expected value = 0.8204.

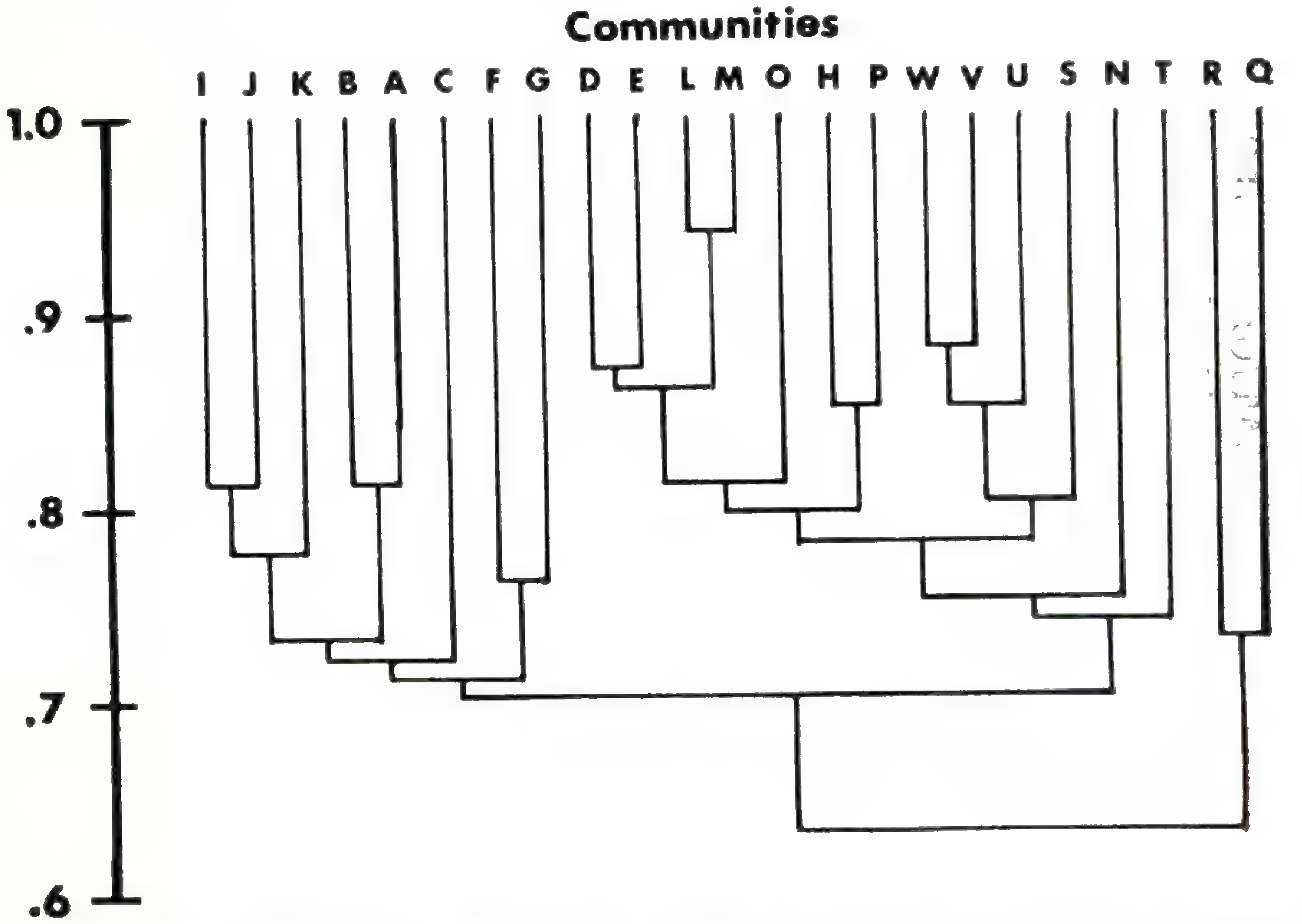


Fig. 29. Population similarity based on the herbaceous species present in the community. Sokal and Michener's coefficent clustered by the unweighted pair-group method. Mean expected value = 0.8204.

TABLE 6. POPULATION ECOLOGY OF TWENTY-THREE POPULATIONS OF *CARDAMINE BULBOSA* AND/OR *C. DOUGLASSII*

Population	Species*	Total Abundance Per Acre (Ab.)	Total Basal Area in Sq. In. Per Acre (BA)	Importance Value (BA+BA+Ab) ÷ 3	Percent Seedling	Abundance Percent Sapling	Percent Canopy	Average Ph	Percent Water
A	*D*B	2346	20,599	14,515	43.75	34.7	5.6	6.99	100
B	*D*B	1082	18,990	13,021	52	24	24	7.08	95
C	*D*B	1201	13,336	9,291	81	13	5	7.08	87
D	D	2673	47,534	32,580	44	26	11	6.36	63
E	D	1424	18,524	12,824	51	30	17	5.8	84
F	D	1601	38,417	26,145	51	41	7	6.47	57
G	D	1645	20,287	14,073	59.0	34.8	6.2	5.9	71.86
H	DB	1389	4,724	3,612	50	49	1	8.15	60
I	D	1144	17,892	12,309	46	46	8	7.3	38
J	*D*B	1092	12,145	8,461	51	37	11	8.6	33
K	D	2142	25,578	17,766	66	22	11	6.45	51
L	B	1109	19,948	13,668	70.4	18.5	11.1	—	100
M	B	369	21,818	14,668	33	22	44	—	100
N	B	1591	16,433	11,486	73.25	22.1	4.65	—	46.4
O	B	1085	44,411	29,969	68	18.7	13.3	6.1	100
P	*B*D	630	7,922	5,491	75.7	13.5	10.8	5.73	100
Q	B	1498	8,154	5,935	72.8	20.3	6.7	7.3	67
R	B	26	46.5	40	0	100	0	7.5	100
S	B	92	2,531	1,718	80	20	0	7.24	100

T	B	1084	28,337	19,253	54.5	40.9	4.5	6.94	100
U	B	10,418	14,900	13,406	92.5	7.2	0.6	5.96	100
V	B	1642	3,088	2,606	83	17	0	—	100
W	B		mowed field					5.7	

*B = *C. bulbosa*
D = *C. douglassii*
Italics indicate that the species is most abundant in that community

group tend to be more open with nearly 100 percent water present whereas the larger group has large trees and tends to be drier. Three groups may be distinguished by the unweighted pair-group method (Fig. 29). While these groups are based on the presence and absence of various species, there is no apparent ecological factor associated with the separation of the communities in this manner (Table 6).

Herbaceous species associated with *Cardamine bulbosa* (Jaccard's coefficient) appear to be different from those associated with *C. douglassii.* The ten highest association values of species found with *C. bulbosa* and *C. douglassii* are different for the herbaceous species, although the almost ubiquitous *Rhus radicans* and *Parthenocissus quin-*

TABLE 7. HERBACEOUS SPECIES WITH THE HIGHEST ASSOCIATION (JACCARD'S) WITH *CARDAMINE BULBOSA* AND *C. DOUGLASSII*[1]

Species	Association
Association with *Cardamine bulbosa*	
Galium aparine	.345
Parthenocissus quinquefolia	.340
Impatiens biflora	.338
Symplocarpus foetidus	.316
Rhus radicans	.294
Eupatorium perfoliatum	.243
Urtica dioica	.220
Caltha palustris	.205
Angelica atropurpurea	.195
Scirpus atrovirens	.189
Association with *Cardamine douglassii*	
Geum vernum	.593
Osmorhiza claytoni	.583
Galium aparine	.564
Viola papilionacea	.556
Cryptotaenia canadensis	.500
Parthenocissus quinquefolia	.487
Rhus radicans	.472
Amphicarpa bracteata	.444
Claytonia virginica	.407
Aster sp.	.360

[1]*C. bulbosa* with *C. douglassii* = .130

quefolia are found with both species (Table 7). When determining which species are most characteristically associated with any one particular species habitat, one cannot consider the absence of a species from an area as being as important as its presence. For this reason it is thought that Jaccard's coefficient best describes the species associated or characteristically found with either *C. bulbosa* or *C. douglassii.*

Jaccard's coefficient (Table 7) shows only a few species highly associated with both *Cardamine douglassii* and *C. bulbosa.* This would be expected if the two species differed in ecological requirements.

Table 8 shows the ten herbaceous species which have the greatest difference between the association with *Cardamine bulbosa* and the association with *C. douglassii.* These may be considered as differential indicators to be used in identifying the species of *Cardamine* expected to be found within a given area. However, one should not assume that all of these species must be present with either *C. bulbosa* or *C. douglassii.*

The importance percentages (Table 9) of the woody species fail to show any clear cut habitat difference between populations of *Cardamine bulbosa* and *C. douglassii.* Close examination, however, does show a dissimilarity of the *C. bulbosa* communities on and off Wisconsin glaciation zones. *Acer saccharum* and *Ulmus americana* are more characteristic of *C. douglassii* and unglaciated *C. bulbosa* communities.

Analysis of both the woody and herbaceous vegetation fails to completely separate populations containing *Cardamine bulbosa* from those containing *C. douglassii.* The R-mode analysis of the herbaceous vegetation does indicate particular plant species commonly associated with one species but not the other. This is an indication of some ecological differences between *C. bulbosa* and *C. douglassii.* That this isolation mechanism is not complete may be seen by the communities in which both *Cardamine* species are found.

TABLE 8. HERBACEOUS SPECIES WITH THE MOST DIFFERENCE BETWEEN THEIR ASSOCIATION (JACCARD'S) WITH *CARDAMINE BULBOSA* AND THAT OF *C. DOUGLASSII*

Species	*Association values* D	B	Difference
Association with *Cardamine bulbosa*			
Symplocarpus foetidus	.121	.316	.195
Scirpus atrovirens	0.0	.189	.189
Carex stipitata	0.0	.179	.179
Sagittaria latifolia	0.0	.162	.162
Typha latifolia	0.0	.162	.162
Carex laxiflora	0.0	.154	.154
Boehmeria cylindrica	0.0	.135	.135
Caltha palustris	.063	.205	.142
Onoclea sensibilis	.032	.154	.122
Senecio aureus	.067	.184	.117
Eupatorium perfoliatum	.138	.243	.105
Association with *Cardamine douglassii*			
Geum vernum	.593	.143	.450
Osmorhiza claytoni	.583	.133	.450
Viola papilionacea	.556	.146	.410
Cryptotaenia canadensis	.500	.156	.344
Amphicarpa bracteata	.444	.130	.314
Hystrix patula	.333	.023	.310
Campanula americana	.320	.022	.298
Aster sp.	.360	.068	.292
Sanguinaria canadensis	.333	.071	.262
Polymnia canadensis	.250	0.0	.250
Claytonia virginica	.407	.159	.248

In general there is separation, as indicated in the dendrograms, between the populations of *Cardamine bulbosa* found in swampy conditions and those of Wisconsin glaciation. Populations of *C. douglassii* with or without *C. bulbosa* seem to cluster together.

The analysis of the woody and herbaceous vegetation, which shows a tendency of *Cardamine douglassii* containing communities to cluster together, is a strong indication of the specificity of *C. douglassii* for a particular habitat. *Cardamine bulbosa,* on the other hand, appears to be quite

variable as to habitat, with a much larger range of habitat conditions under which it is capable of undergoing ecesis.

Herbaceous species are found to be associated with *Cardamine bulbosa* at a lower level than with *C. douglassii.* This fact may also be interpreted to mean that the particular study areas containing *C. bulbosa* varied more than those containing *C. douglassii* and that the resulting associations are due to sampling error or the fact that the ecology of *C. bulbosa* is more variable than that of *C. douglassii.*

MORPHOLOGY

To be able to more fully understand the evolutionary relationships between and within *Cardamine douglassii* and *C. bulbosa,* it was considered necessary to take a closer look at the morphological similarities and differences within the taxa. Plants for morphological study were selected at random from within each population. Twenty-two characters were measured on each plant. Seven of these characters were averages, such as the length of the pubescence, length of petals, etc. Through the use of various indices the number of characters was increased to thirty-one (Table 10).

Three measurements were made to the nearest millimeter (Character Numbers 2, 3, 4) and three (number of branches, number of leaves, number of hairs per mm^2) were meristic in nature. Length of pubescence and number of hairs per square millimeter were calculated using an ocular micrometer. Other measurements were made with calipers to the nearest .001 mm.

When the plants were collected in the field, one or two flowers were picked. Since petal size may vary depending on the age of the flower, the flowers used were all of about the same age. A flower was dissected, the parts placed on ozalid paper and then exposed to light. Later exposure to ammonium hydroxide caused the shaded portion that had been covered by the flower parts to become dark. Measurements of the images were made with a Bausch and Lomb measuring magnifier to the nearest tenth of a millimeter.

TABLE 9. IMPORTANCE PERCENTAGES (GREATER THAN 5%) OF WOODY SPECIES IN THE TWENTY-THREE COMMUNITIES

Community Letters	R	V	U	T	M	Q	S	P	N	L	O	E	G	B	A	F	K	I	D	H	J	C
Population Number	8	11	3	9		7		4	10	1	6	15	17		12,13	16	20		14	5,18	19	14
Species:																						
Salix nigra	100					42.7	53.1															
Fraxinus americana					91.8	10.6	31.7		6.9	34.7	8.9	12.7		10.2			17.5	59.1		7.0	29.8	
Juglans nigra							7.1									8.0					19.1	
Acer negundo						15.4		36.5							22.7	9.4				17.2		
Cornus amomum		68.9				22.6																
Quercus macrocarpa						6.8																
Thuja occidentalis				22.3																		
Lindera benzoin				6.5				28.3	14.3		7.4											
Fraxinus pennsylvanica				29.1				26.1							36.0							
Juglans cinerea				36.3																		
Platanus occidentalis									8.4													37.8
Carpinus caroliniana									13.5						5.2		11.4					

Acer saccharum								44.1			5.4	6.8		8.4			8.4	21.3		
Ulmus americana							8.5	12.8			30.4	7.9							30.1	20.8
Alnus rugosa		62.4																		
Acer rubrum		28.1								64.8										
Rhus vernix		7.9																		
Carya ovata										8.1	10.2	27.8								
Quercus alba										22.3						30.4				
Quercus falcata									10.0											
Viburnum dentata	21.5																			
Salix sp.	8.5																			
Acer saccharinum														5.6						
Ostrya virginiana												9.1		9.5			5.3			
Cercis canadensis														16.4			6.0			
Ulmus fulva														16.7		5.5	5.3	56.6		
Liriodendron tulipifera													8.4							
Celtis occidentalis															14.4					7.8
Quercus bicolor															6.2					
Prunus serotina															9.6					
Carya cordiformis													12.4		34.5					
Corylus americana															8.6					
Quercus borealis												30.5	6.2							
Crataegus sp.												5.9								
Gleditsia triacanthos																	26.5			
Cornus florida													6.4							
Sassafras albidum													35.4							

TABLE 10. CHARACTERS USED IN THE MORPHOLOGICAL STUDY

1. Number of branches
2. Height to first pedicel from the base of the stem (cm)[1,2]
3. Height to first leaf from the base of the stem (cm)
4. Height to second leaf from the base of the stem (cm)[2]
5. Length of petiole of first leaf (cm)
6. Length of lowest cauline leaf (cm)[2]
7. Width of lowest cauline leaf (cm)
8. Length of petiole of second leaf (mm)
9. Length of second leaf (cm)[1,2]
10. Width of second leaf (cm)
11. Least width of second leaf (cm)
12. Number of cauline leaves[1,2]
13. Height of plant ÷ number of branches (no. 2 ÷ no. 1)[2]
14. Height of first leaf ÷ petiole height (no. 3 ÷ no. 2)[2]
15. Leaf one: petiole-blade index (no. 5 ÷ no. 6)
16. Leaf one: leaf index (no. 7 ÷ no. 6)[2]
17. Leaf two: petiole-blade index (no. 8 ÷ no. 9)
18. Leaf two: leaf index (no. 10 ÷ no. 9)[1,2]
19. Height ÷ number of leaves (no. 2 ÷ no. 12)
20. Number of hairs per mm (avg.)[1,2]
21. Average pubescence length (0.01mm)[1,2]
22. Width of stem (mm)[2]
23. Length of calyx (avg.) (mm)
24. Length of petals (avg.) (mm)[1,2]
25. Width of petals (avg.) (mm)[2]
26. Petal index (no. 25 ÷ no. 24)[1,2]
27. Filament length (avg. of long stamens in mm)[2]
28. Pistil length (mm)[2]
29. Gyno-andro index (no. 27 ÷ no. 28)[1,2]
30. Leaf two width index (no. 11 ÷ no. 10)[1,2]
31. Color petals (from 1 to 7)[1]

[1]Characters studied in comparison of intrapopulational differences of *C. bulbosa*.
[2]Characters used in calculating Davidson and Dunn coefficient.

Since this was a study of the biosystematics of *Cardamine bulbosa* and *C. douglassii,* it was felt that the inclusion of hybrids collected in a population could be misleading when comparing the populations morphologically. This was a problem in only one community, near Bowling Green, Ohio, where both species and their putative hybrids occur quite commonly. Hybrids were determined based on their intermediate pubescence length and intermediate flowering time, and plants judged to be hybrids were eliminated from the morphological species comparison. This is, then, an attempt to compare only the so called "pure" species.

The recommended sample size for similar taxonomic treatments is from 15-25 individuals (Cazier & Bacon, 1949). Pimentel (1958) investigated the effect of sample size on the range of confidence limits. He found a decrease in the size of the confidence limits with an increase in sample size. About fifteen samples are required to stabilize these limits. A partially successful attempt was made in this study to collect a minimum of fifteen plants from each population. In three populations of the twenty populations (Table 1) the scarcity of specimens necessitated collections of less than fifteen plants. These areas were Pymatuning Lake, Ohio; Camp Hook, Ohio; and at Pulltight Springs, Missouri (population numbers 11, 14, and 2).

Physiogeographic variability may be a significant factor influencing plant morphology. This indicates the importance of equidistance between sample areas. Frequent sampling in similar nearby habitats may represent wasted time and energy while too infrequent sampling may divide a gradual cline into several distinct taxa. Of necessity, most of the twenty populations studied were in southwestern Ohio with scattered areas in northern Ohio, Kentucky and Missouri. Although this cannot be considered a complete study of both taxa, it is at least respresentative of those plants in the mid-West.

The mean, standard deviation, maximum and minimum were computed for the characters in the twenty populations (Hart, 1972, Appendix 11). Significant differences or similarities between populations were established using an analysis of variance for each particular character (Table 10). For this test, data for the particular character were used for all plants measured with a maximum of thirty plants per population.

When the F value was significant ($0.01 \leq p \leq 0.05$) or highly significant ($p \leq 0.1$) the Student Newman Keuls (SNK) Multiple Range Test (Woolf, 1968) was used to compare the means and show where the similarities and differences were located. The probability level of rejecting the null hypothesis was 0.05.

Petal color was studied by comparing specimens with other specimens instead of with a color chart (Kerlan, 1965). Three different colored petals from three different plants were chosen as standards. One petal was very light pink, another pinkish-purple and the third, rather dark purple. Any specimen lighter than light pink (2) was considered white (1), while those darker than purple (6), were reported as dark purple (7). The measurement of petal color necessitated the use of non-parametric methods which are used when one is concerned with the distribution of variates and not the specific parameters or when there are different distributions or variances involved. The Kruskal-Wallis test (Siegel, 1956) which is based upon the ranking of the variates and the assumption that if different populations are not different from each other, the ranks should be approximately the same (Sokal & Rohlf, 1969).

The number of branches was found to be a useful character by Stuckey (1962). Its interspecific and intraspecific importance was tested with the Kruskal-Wallis test as was petal color. Petal color has also been tested with analysis of variance and the multiple range test. This was done, even though it is not statistically valid, in an attempt to show which populations differed.

Simple regression based on the character means of each population was computed with selected morphologic and ecologic characters. Both interspecific and intraspecific regression were done with all combinations.

Simple regression is a means of measuring a linear relationship between two characters assuming that one is dependent upon the other. The regression establishes the form (positive or negative) and significance of this relationship between two variables. The presence of a significant relationship between two variables should not be assumed to indicate any biologic dependence of one upon another as both variables may be dependent on a third, unknown variable.

Multiple regression (Bliss, 1967) was used on a selected number of morphological characters in an attempt to determine which morphologic and/or ecologic characters seem to be most important in explaining the variation of a particular character. Multiple regression estimates the total relation between one variable and each predicting variable.

Seemingly logical variables (Hart, 1972, Appendix 14) were tested against the one character Y. Those characters seeming most important in explaining the variability of character Y were retested and retested again each time eliminating the least important variable. Upon elimination of those characters which could least explain the variability of Y, one to a few characters will usually remain. Elimination of any of these remaining characters causes a drastic drop in the F value and a decrease in the Coefficient of Determination (r^2) which is the per cent of the variation of Y which the remaining characters explain.

Multiple regression analyses of five ecological characters and each of the morphological characters making up the two major groups of correlated *Cardamine bulbosa* characters (Fig. 38) were attempted. These analyses were performed on the premise that one of these two groups might be more strongly influenced by certain ecologic factors than the other.

A Model I linear regression is used when a dependent or random variable (Y) is correlated with and varies on an independent or fixed variable (X). When both variables are dependent, the rare Model II linear regression is assumed. Computations for both models are identical.

Two similarity coefficients were used in analysis of the twenty populations of *Cardamine douglassii* and *C. bulbosa.* Each population was considered as being an operational taxonomic unit (OTU). The correlation coefficient and distance coefficient were used for comparing the populations based on thirty-one morphological characters. The programs, written in the APL/360 languages according to Sokal and Sneath (1963) and Sneath and Sokal (1973) have the missing data option. Population means of the thirty-one characters were first standardized (Sokal & Sneath, 1963) and then the similarity coefficients were calculated.

The hybrid index was calculated based on four relatively good diagnostic characters. It was felt that these characters (pubescence length, plant height, flower color, and blooming time) were the best characters in distinguishing *Cardamine bulbosa* from *C. douglassii.* In each of these four characters, the typical *C. bulbosa* condition was set at from one to four while *C. douglassii* was set at zero (Fig. 41). Only the plants collected by the random method were used.

It is important to realize that the value given to the fourth character in this study (blooming time) was based on the number of flowers in bloom or yet to bloom divided by the total number of buds, flowers and fruits, when compared to one or the other parental species. Populations from communities in which only one species of *Cardamine* was found were assumed to be typical for that species.

As random samples of the two species were collected at different times without any knowledge of the relative abundance of each of the species, no attempt should be made to predict the relative abundance of the two species from the hybrid index percentages.

In this investigation a number of statistical tests were used to determine and interpret morphological relationships and/or differences.

The APL/360 computer was used with some of the functions written by the authors (TWH) expressly for this study.

To identify the inter- and intrapopulational variation of *Cardamine bulbosa* and *C. douglassii* the analysis of variance and the SNK Multiple Range Test (Table 11) were computed on ten of the thirty-one characters measured. In interpreting (Table 11) each multiple range test, all means which are over any given line are not significantly (0.05 level) different from each other. Means which are not over the same continuous line are significantly different.

Standard deviation, mean and range are plotted for pubescence length, plant height (Figs. 30, 31), the number of hairs per mm^2 (Fig. 32), and the number of cauline leaves (Fig. 33). Pubescence length (Fig. 30) appears to be a character which can always be used to identify an individual plant species. Population number 13 (*Cardamine douglassii*) has a significantly shorter pubescence length (Fig. 30) than 5 of the 7 other populations of *C. douglassii.* The difference in pubescence lengths of plants grown under controlled greenhouse conditions can be seen in Fig. 34. The pubescence length of the known hybrid is noticeably intermediate between that of *C. bulbosa* and *C. douglassii.* Plant height is also a good diagnostic character (Fig. 31). While significant, plant height does show considerable overlap and cannot be used as the only identifying character.

Again, the Bowling Green population of *Cardamine douglassii* (no. 13) is unusual because of its petal index. These plants (Table 11), on the average, have the largest index of all, significantly different from the southern ($n = 32$) populations of that species.

The Student Newman Keuls Multiple Range Test (Table 11) indicates that the length of the second leaf is not an important character distinguishing the two species. How-

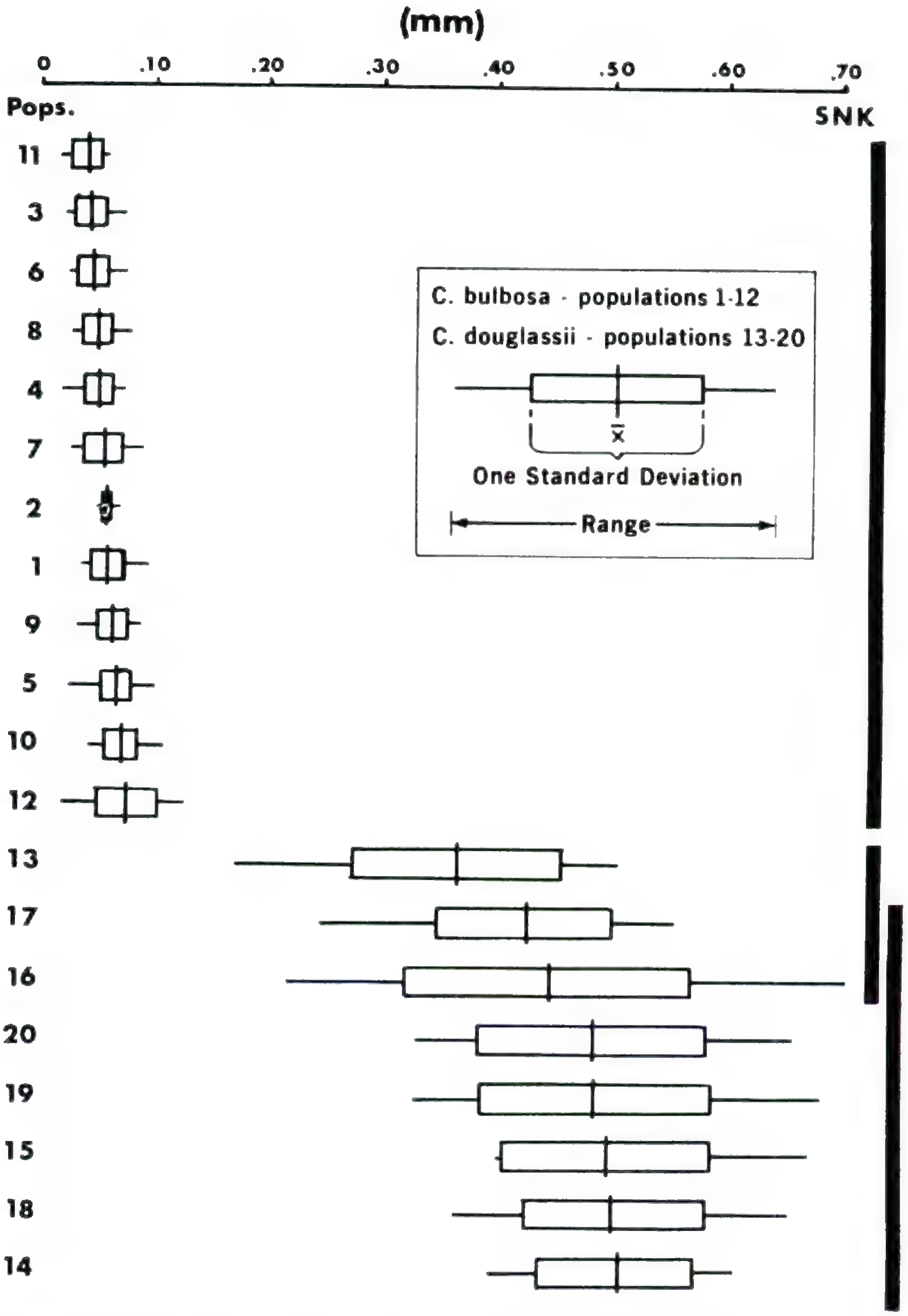


Fig. 30. Pubescence length as depicted by Analysis of Variance and Student-Newman-Keuls Multiple Range Test (SNK).

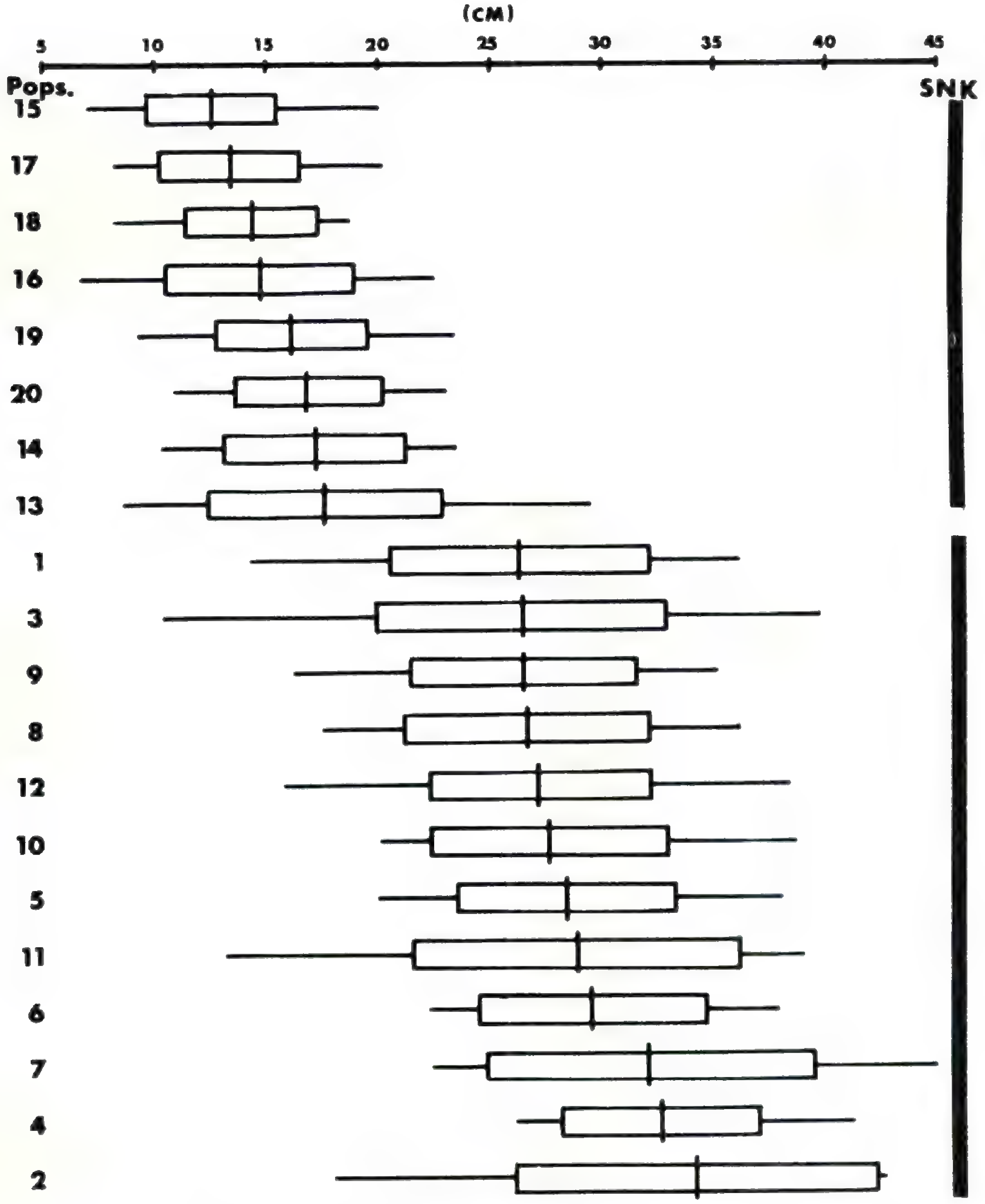


Fig. 31. Plant height as depicted by Analysis of Variance and Student-Newman-Keuls Multiple Range Test (SNK). See Figure 30.

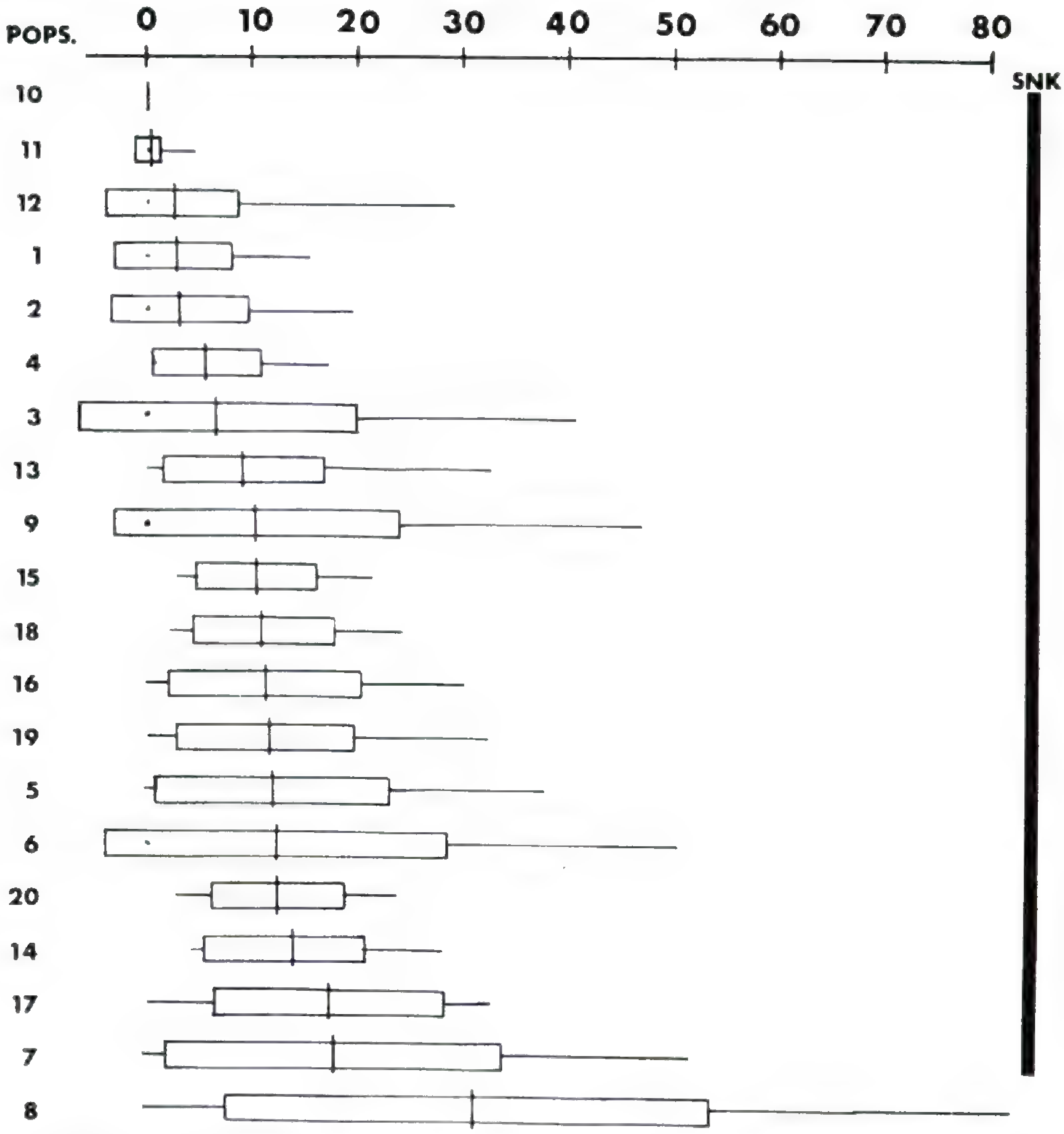


Fig. 32. Number of hairs per square millimeter as depicted by Analysis of Variance and Student-Newman-Keuls Multiple Range Test (SNK). See Figure 30.

ever, all *Cardamine douglassii* populations have shorter average leaves than does *C. bulbosa.* The two northern, polyploid *C. douglassii* populations have larger leaves than the other *C. douglassii.* Forma *fontinalis* of *C. bulbosa* has the longest leaves of all populations studied but unlike the number of leaves (Fig. 33), this character difference proved to be insignificant.

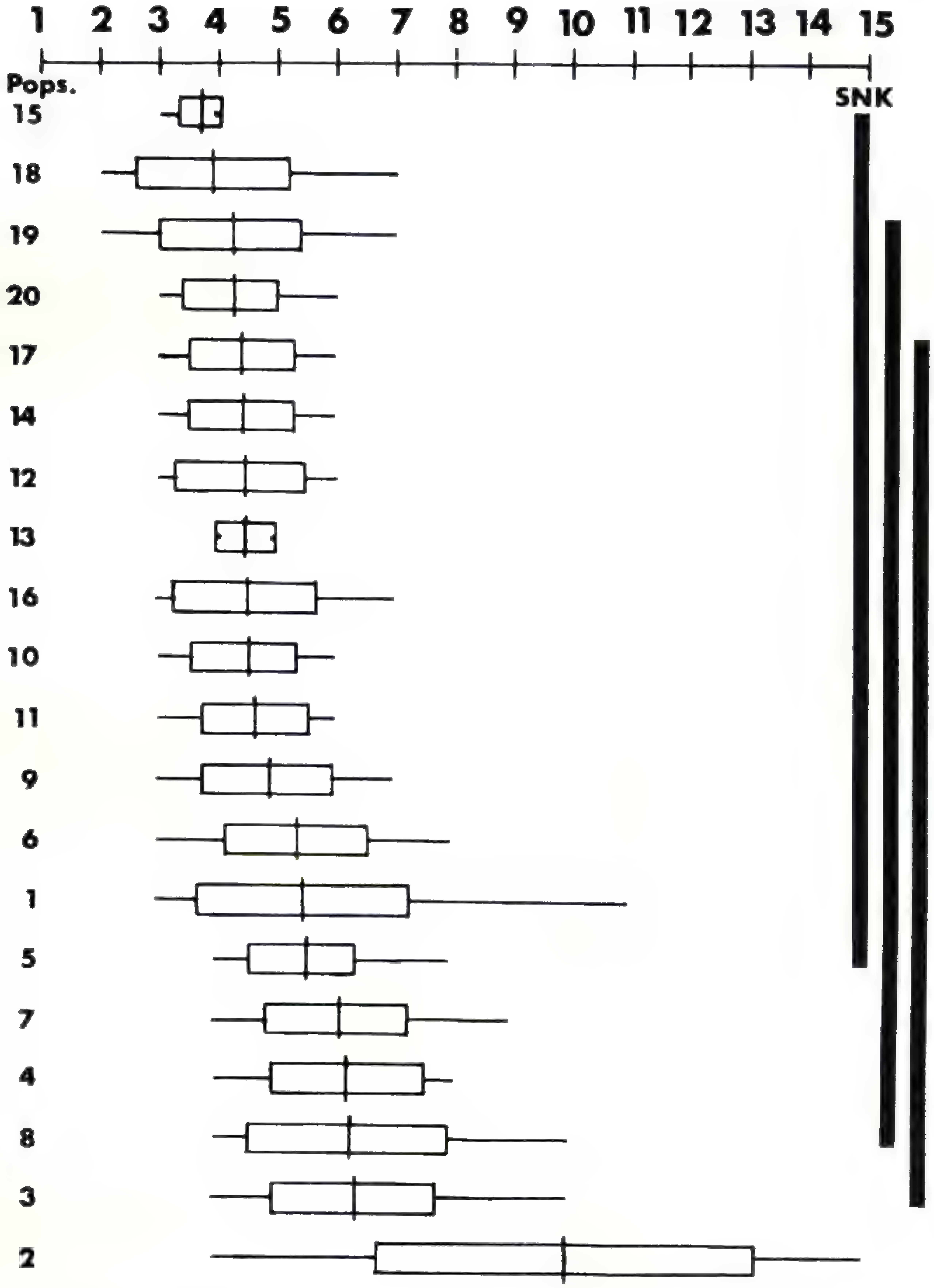


Fig. 33. Number of leaves per stem as depicted by Analysis of Variance and Student-Newman-Keuls Multiple Range Test (SNK). See Figure 30.

TABLE 11. ANALYSIS OF VARIANCE AND STUDENT NEWMAN KEULS TEST (0.05 LEVEL) OF *CARDAMINE BULBOSA* AND *C. DOUGLASSII* USING TEN CHARACTERS.

Character 2 — Plant Height — f = 33.2

Pop. No.	15	17	18	16	19	20	14	13	1	3	9	8	12	10	5	11	6	7	4	2
N	15	20	22	15	23	15	13	30	18	21	22	16	22	19	20	14	17	17	15	8
$\bar{x}$	12.55	13.35	14.3	14.71	16.12	16.75	17.15	17.36	26.27	26.31	26.4	26.5	27.04	27.47	28.25	28.69	29.47	31.9	32.45	34.01

Character 9 — 2nd Leaf Length — f = 17.37

Pop. No.	17	18	14	19	20	16	9	15	13	8	10	1	4	3	11	5	7	12	6	2
N	20	22	13	23	15	15	21	15	30	16	19	18	14	21	13	20	17	22	17	8
$\bar{x}$	1.76	1.97	1.99	2.01	2.02	2.05	2.07	2.08	2.29	2.46	2.52	3.12	3.30	3.32	3.44	3.65	3.74	3.77	4.11	4.55

Character 12 — Number of Leaves — f = 14.89

Pop No.	15	18	19	20	17	14	12	13	16	10	11	9	6	1	5	7	4	8	3	2
N	15	22	23	15	20	13	22	30	14	19	14	22	17	18	20	17	15	16	21	8
$\bar{x}$	3.67	3.91	4.26	4.27	4.45	4.46	4.5	4.53	4.57	4.58	4.71	4.96	5.41	5.5	5.6	6.18	6.33	6.38	6.48	10

Character 18 — Leaf 2 index — f = 9.422

Pop. No.	8	9	6	7	10	5	11	12	20	18	14	4	3	19	2	17	16	15	13	1
N	16	21	17	17	19	20	13	22	15	22	13	14	14	23	8	20	15	15	30	18
$\bar{x}$	.36	.41	.41	.42	.45	.46	.46	.47	.48	.50	.50	.50	.50	.51	.55	.55	.58	.63	.65	.83

Character 20 — No. of Hairs — f = 7.7

Pop. No.	10	11	12	1	2	4	3	13	9	15	18	16	19	5	6	20	14	17	7	8
N	19	14	22	18	8	15	21	30	22	15	22	15	23	20	17	15	13	20	17	16
$\bar{x}$	.000	.033	2.52	2.77	3.09	5.62	6.61	9.65	10.2	10.4	10.9	11.4	11.6	12.1	12.5	12.6	13.2	17.6	18.2	30.8

Character 21 — Pubescence Length — f = 182.6

Pop. No.	11	3	6	8	4	7	2	1	9	5	10	12	13	17	16	20	19	15	18	14
N	11	17	17	16	14	17	5	17	18	19	19	22	30	20	15	15	23	15	22	13
$\bar{x}$	4.37	4.49	4.85	5.14	5.28	5.86	6.08	6.12	6.51	6.9	7.19	7.85	36.94	42.58	44.55	48.51	48.64	49.68	50.39	50.81

TABLE 11. (Continued)

Character 24					Petal Length					f = 16.217										
Pop. No.	8	9	6	4	7	5	14	10	19	18	20	16	15	17	11	1	13	3	2	12
N	16	22	17	15	17	20	13	19	23	22	15	15	15	18	12	18	21	21	5	20
$\bar{x}$	7.68	8.04	8.08	8.51	8.61	8.68	9.24	9.30	9.72	9.90	10.06	10.18	10.23	10.34	10.35	10.55	10.70	10.80	11.03	12.32

Character 26					Petal Index					f = 10.37										
Pop. No.	10	20	17	16	11	5	2	19	14	4	18	8	6	9	15	7	12	1	3	13
N	19	15	18	15	12	20	5	23	13	15	22	16	17	22	15	17	20	18	21	1
$\bar{x}$	.378	.397	.403	.403	.416	.416	.416	.417	.425	.427	.428	.435	.467	.474	.479	.494	.50	.530	.537	.591

Character 30					Leaf 2 Width Index					f = 6.336										
Pop. No.	12	14	17	20	15	10	19	18	13	16	5	6	8	9	7	4	11	1	2	3
N	22	13	20	20	15	19	22	22	30	15	19	17	16	22	17	15	14	18	8	30
$\bar{x}$	.764	.782	.796	.801	.803	.805	.813	.821	.827	.837	.847	.863	.871	.872	.906	.926	.938	.943	.955	.981

Character 31					Color					f = 59.6										
Pop. No.	1	2	3	5	6	16	11	4	9	7	12	8	18	19	17	20	14	15	13	16
N	18	8	21	19	17	19	12	15	22	17	20	16	16	22	20	15	13	15	29	15
$\bar{x}$	1	1	1	1	1	1	1	1.13	1.22	1.59	1.65	1.94	3.38	3.77	4.7	4.73	4.85	5.53	5.69	5.87

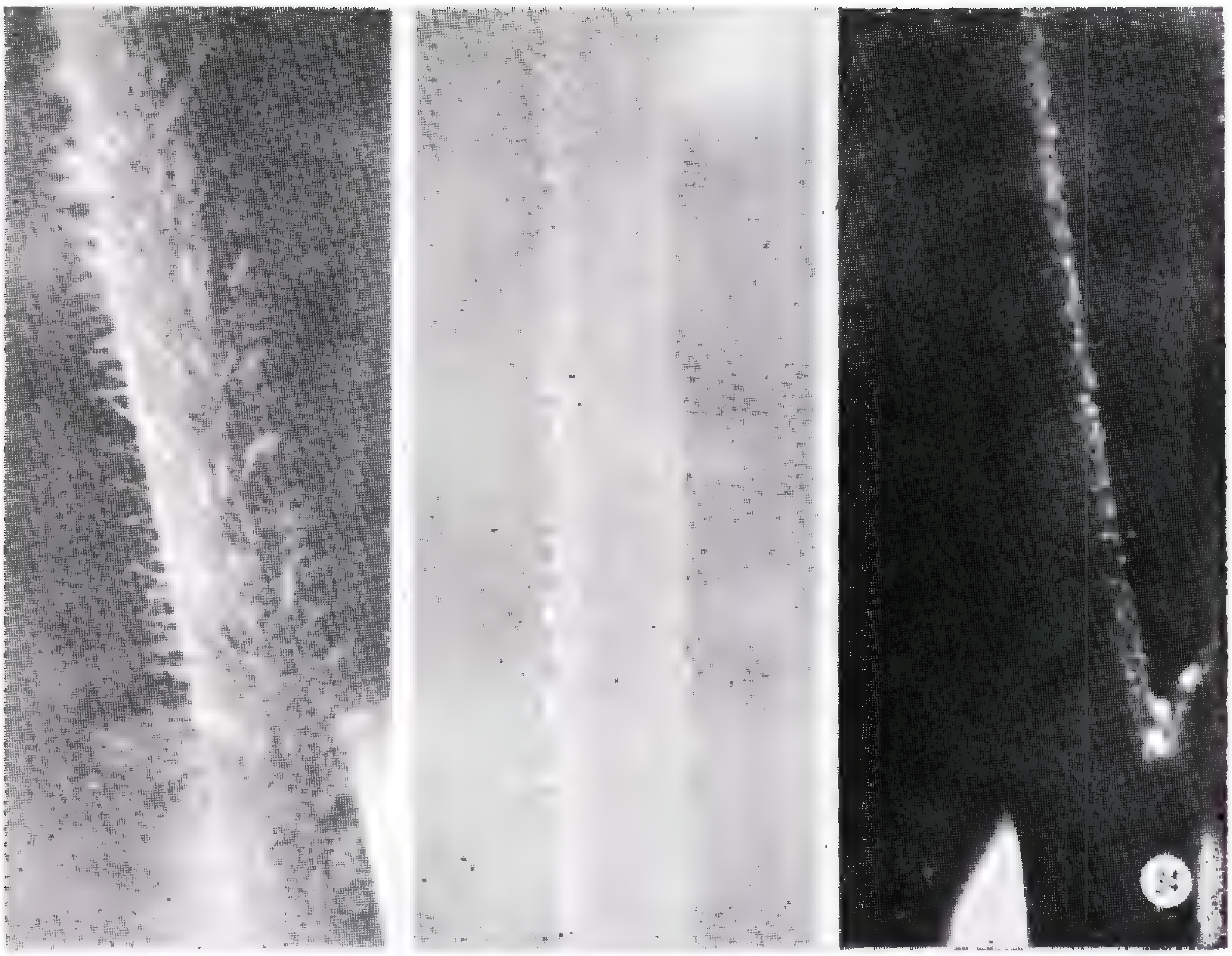


Fig. 34. Left Panel, pubescence in *Cardamine douglassii.* Middle panel, pubescence in known hybrid. Right panel, pubescence in *C. bulbosa.*

Branch number and petal color, two nonparametric characters (no. 1 and 31), were found to vary significantly within the twenty populations studied (Table 11) when tested with the Kruskal-Wallis One Way Analysis of Variance Test. Visualization of the location of the important differences can be made using Figures 35 and 36 where the frequency of the petal color index and the number of branches are shown.

Both *Cardamine douglassii* and *C. bulbosa* generally lack branches. However, four populations of *C. bulbosa* average greater than two branches per plant. The multiple range test, used only to demonstrate populational differences and not as an accurate statistic, shows a species separation by petal color. The flowers of all *C. bulbosa* average white (1) to light pink (2) while *C. douglassii* is darker in color. Three *C. douglassii* populations were significantly darker than all the others.

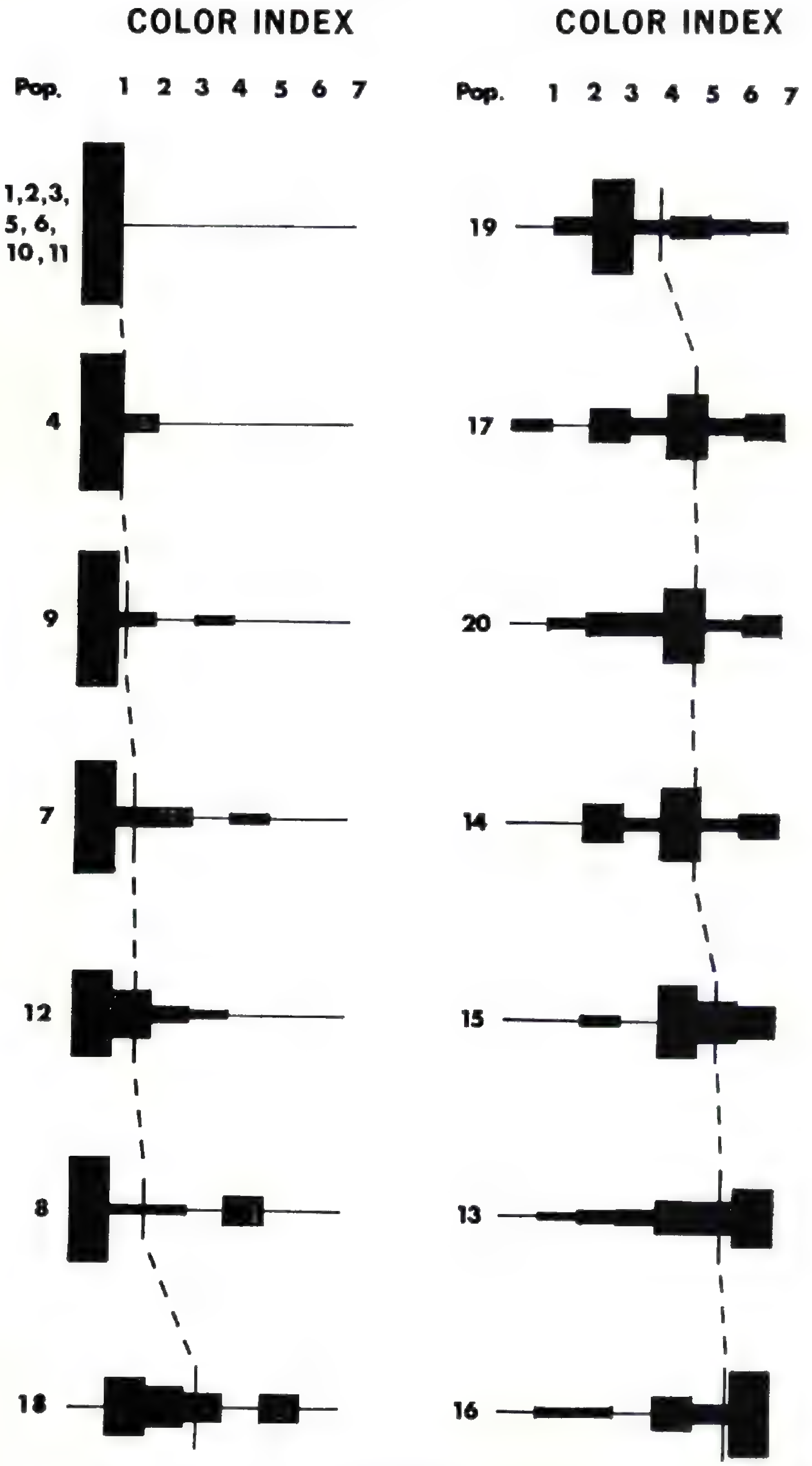


Fig. 35. Color index. The frequency of colors (white = 1, purple = 7) in the population is indicated by the width of the lines. The mean value is indicated by the dotted line. *Cardamine bulbosa* (populations 1-12) and *C. douglassii* (populations 13-20).

TABLE 12. ANALYSIS OF VARIANCE AND MULTIPLE RANGE TEST (0.05) OF *CARDAMINE BULBOSA* USING ELEVEN CHARACTERS.

Character 9				2nd Leaf Length				f = 8.6596				
Pop. No.	9	8	10	1	4	3	11	5	7	12	6	2
N	21	16	19	18	14	21	13	20	17	22	17	8
$\bar{x}$	2.07	2.46	2.52	3.12	3.30	3.32	3.44	3.65	3.74	3.77	4.11	4.55

Character 30				Leaf 2 Width Index				f = 10.36				
Pop. No.	12	10	5	6	8	9	7	4	11	1	2	3
N	22	19	19	17	16	22	17	15	14	11	8	30
$\bar{x}$	.764	.805	.847	.863	.871	.872	.906	.925	.938	.943	.955	.981

Character 24				Petal Length				f = 20.53				
Pop. No.	8	9	6	4	7	5	10	2	11	1	3	12
N	16	22	17	15	17	20	19	6	12	18	21	20
$\bar{x}$	7.68	8.04	8.08	8.51	8.61	8.68	9.30	9.41	10.35	10.55	10.8	12.3

Character 21				Pubescence Length				f = 7.76				
Pop. No.	11	3	6	8	4	7	2	1	9	5	10	12
N	11	17	17	16	14	17	5	17	18	19	19	22
$\bar{x}$	4.36	4.49	4.85	5.14	5.28	5.86	6.07	6.12	6.5	6.9	7.19	7.85

TABLE 12. — Continued.

Character 12				Number of Leaves				f = 12.7				
Pop. No.	12	10	11	9	6	1	5	7	4	8	3	2
N	22	19	14	22	17	18	20	17	15	16	21	8
$\bar{x}$	4.5	4.58	4.71	4.95	5.41	5.5	5.6	6.18	6.33	6.37	6.48	10
Character 20				No. of Hairs				f = 9.08				
Pop. No.	10	11	12	1	2	4	3	9	5	6	7	8
N	19	14	22	18	8	15	21	22	20	17	17	16
$\bar{x}$	.000	.033	2.25	2.77	3.09	5.62	6.61	10.2	12.1	12.5	18.2	30.8
Character 18				Leaf 2 Index				f = 14.91				
Pop. No.	8	9	6	7	10	5	11	12	4	3	2	1
N	16	12	17	17	19	20	13	22	14	21	8	18
$\bar{x}$	.36	.410	.411	.416	.449	.456	.461	.472	.502	.503	.546	.831

Characters 2, 26, 29 and 31 not significant

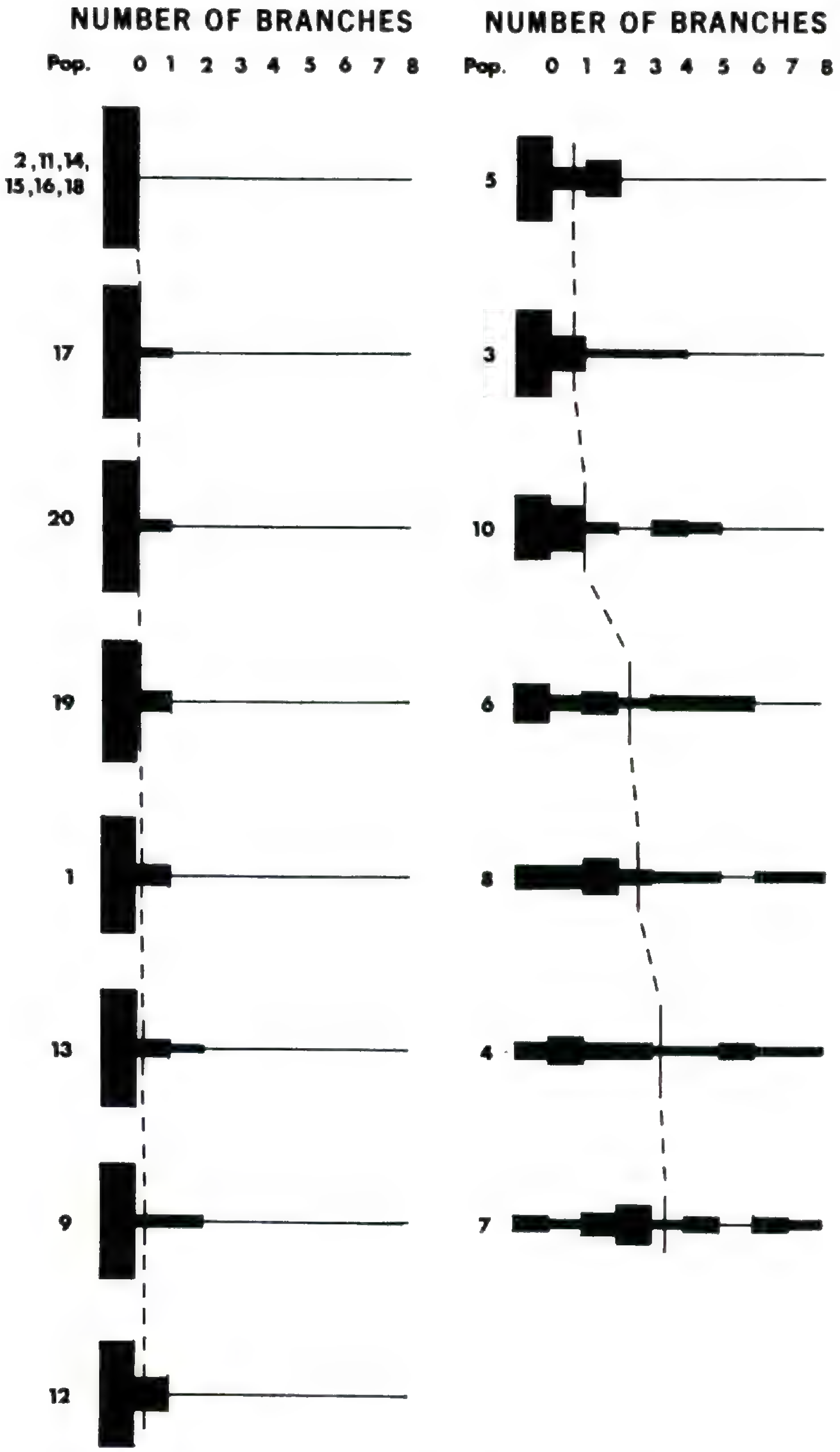


Fig. 36. Number of branches. The frequency of the number of branches in the population is indicated by the width of the line. See Figure 35.

Population differences within *Cardamine bulbosa* were measured using analysis of variance (See Hart, 1972) and a multiple range test (Table 12). Population number 12 has at least two significant differences from all the populations studied (Fig. 37). This population is near Bowling Green, Ohio and consists of scattered clumps of *C. bulbosa* among large numbers of *C. douglassii.* Putative hybrids are relatively common and can be identified by their intermediate flowering time and length of pubescence. They are, however, not included in the statistical study of the populations. Nevertheless, population 12 (Fig. 37) is different from all other populations of *C. bulbosa,* and it varies towards *C. douglassii* in pubescence length, flower color and number of leaves. Population 12 (*C. bulbosa*) differs from most other populations of *C. bulbosa* studied as to petal length and leaf width index of the second leaf.

A second population (no. 8) is outstanding because it differs from other *Cardamine bulbosa* populations (Fig. 37) in having numerous branches, pink petals (Fig. 35) and is a member of chemical race C. It is possible that growth in full sunlight may have accentuated other differences such as the amount of pubescence, petal size, filament length, and pubescence length.

Finally, population 2 is notably different (Fig. 37) from five or more of the other *Cardamine bulbosa* populations. This population of *C. bulbosa* grows almost entirely submerged in cold spring water and was collected in Missouri.

Simple regressions of seventeen morphological characters, using population averages as well as six ecologic measurements, were computed in all possible combinations. Intrapopulational correlations studied by this method indicate that within *Cardamine douglassii* five characters are significantly (0.05) correlated with chromosome number. These characters are the leaf index, number of hairs per sq. mm, average pubescence length, stem width, and the petal index. There is also an indicated relationship of the filament length, stem width and petal color with various ecologic factors. No important or unexpected character

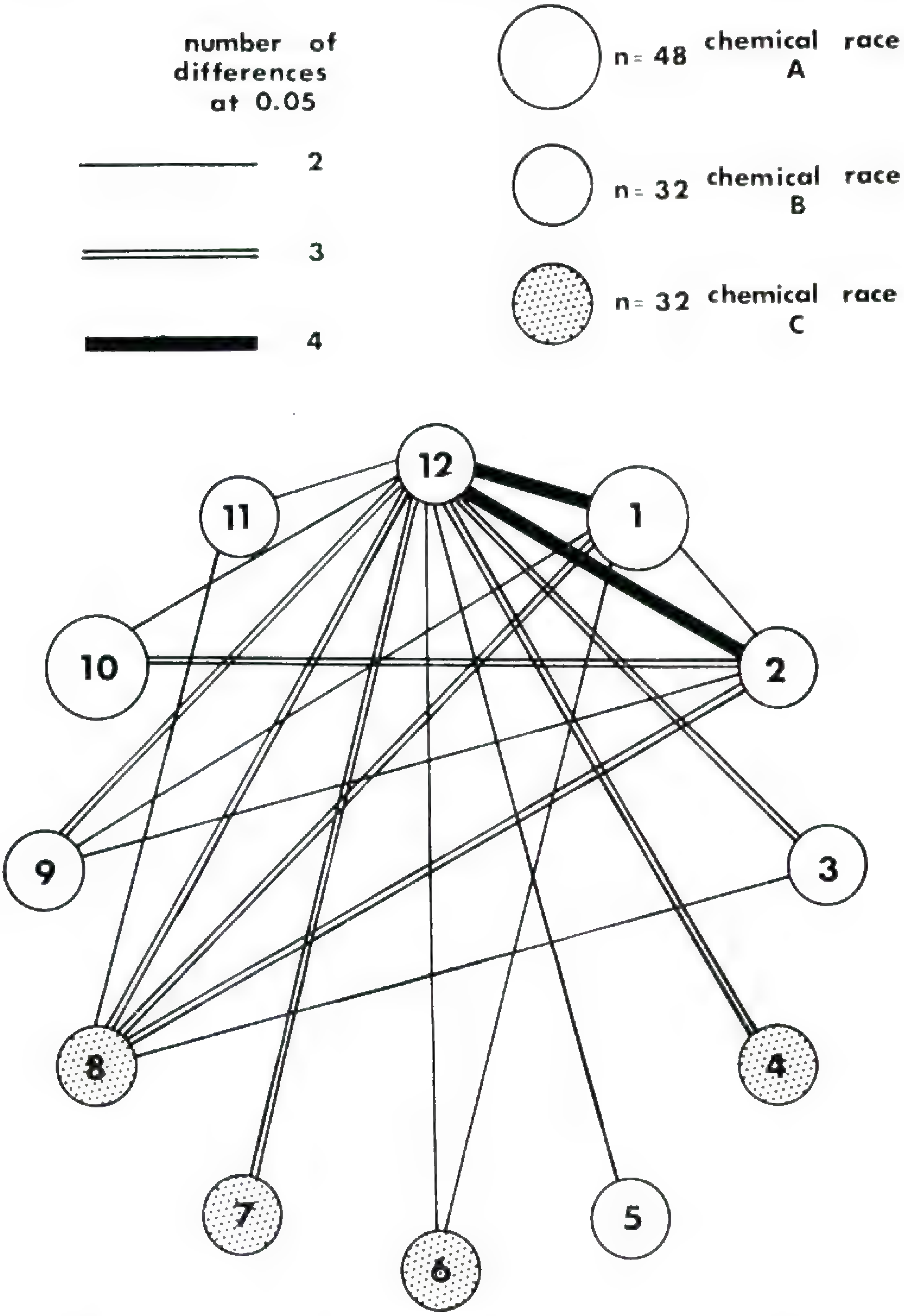
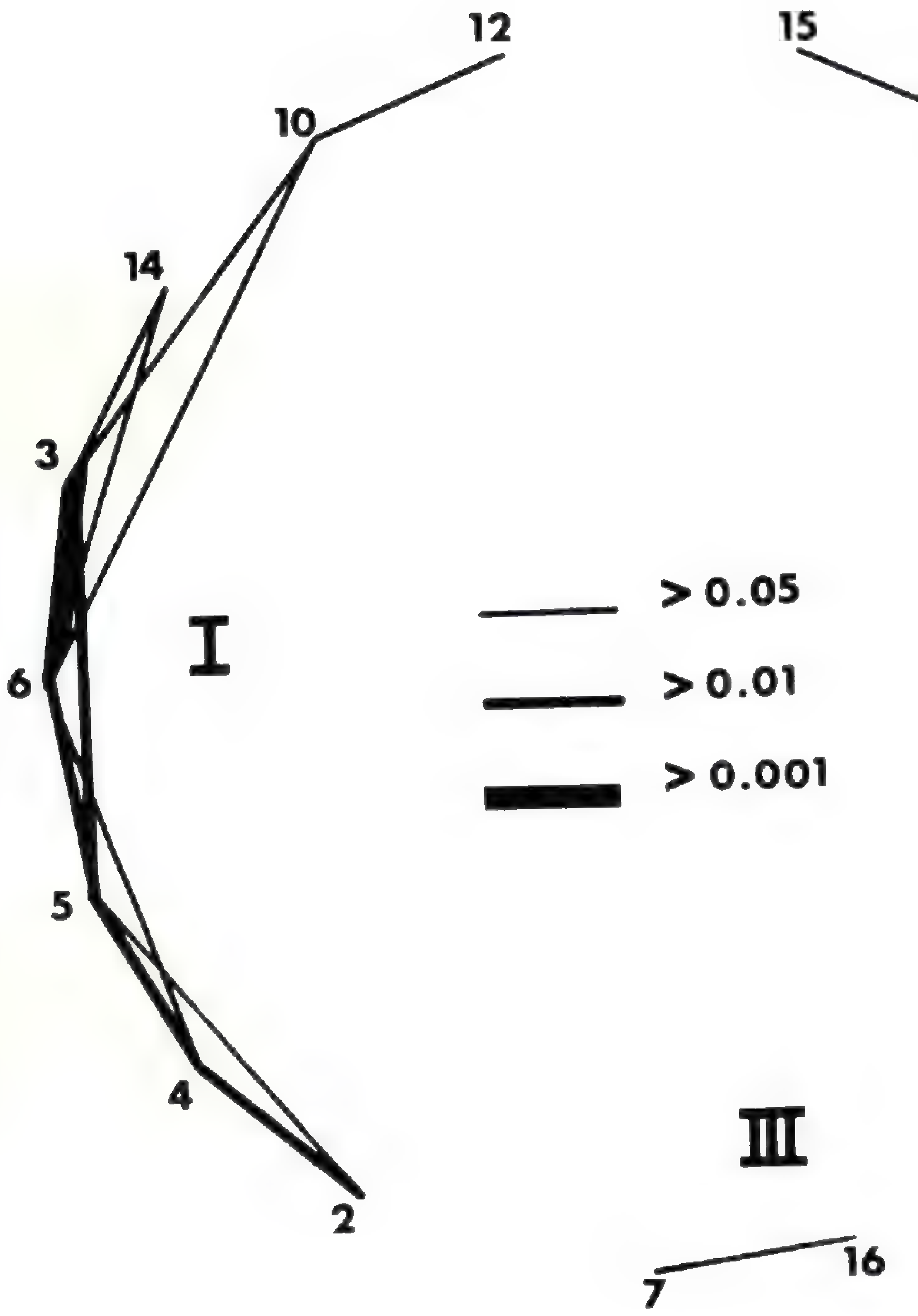


Fig. 37. Summary of the differences (eleven characters) between populations of *Cardamine bulbosa* as shown by the Multiple Range Test.



1. Number of branches
2. Height to first pedical
3. Height to second leaf
4. Length of first leaf
5. Number of cauline leaves
6. Height of first leaf - Height to first pedical
7. Leaf one index (width - length)
8. Number of hairs per mm sq
9. Average pubescence length
10. Stem width
11. Length of petals
12. Petal index
13. Filament length (long stamens)
14. Gyno-andro index (Filament length - pistil length)
15. Petal color
16. Chromosome number
17. Chromatographic pattern

Fig. 38. Character correlations in *Cardamine bulbosa* as shown by simple regression analysis.

correlations were seen when all populations were included in the interpopulational simple regression analysis.

Certain of the twenty-five significant character correlations of *Cardamine bulbosa* as measured by simple regression are of particular interest. The chromatographic pattern, for example, is correlated with branch number, pubescence length, and filament length.

Figure 38 shows all the significant correlation (0.05) levels of the various morphological characters. These correlations appear to be in three groups. The first group is the chromatographic pattern and its associated characters. A second group is those characters dealing with size and the various indices. The third relatively small group indicates a correlation between chromosome number and the leaf index. The multiple regression of the correlated characters. within *Cardamine bulbosa*, with various ecologic factors showed that no significant correlations occurred.

The shaded correlation matrix (Fig. 39) based on twenty populations shows *Cardamine douglassii* (populations 13-20) as being quite similar while *C. bulbosa* (populations 1-12) shows considerable variation within the species. Populations 13 and 14 show a little less similarity than is typical for the other *C. douglassii* groups (Fig. 40). Both of these populations are growing in moist soil with *C. bulbosa* and putative hybrids nearby. However, populations 13 and 14 have different chromosome numbers and are found in different geographical sites in Ohio.

OTU number 12 is a population of *Cardamine bulbosa* growing in northern Ohio and apparently hybridizing with *C. douglassii*. Population number 12 is not very similar to either species.

The distance coefficient failed to produce as sharp a separation between *Cardamine douglassii* (OTU 13-20) and *C. bulbosa* (OTU 1-12) as might be anticipated. OTU's number one and two are not very similar to most other *C. bulbosa*. In both these populations the plants were growing partially submerged in cold spring water. OTU one and ten also have a chromosome number of $n = 48$.

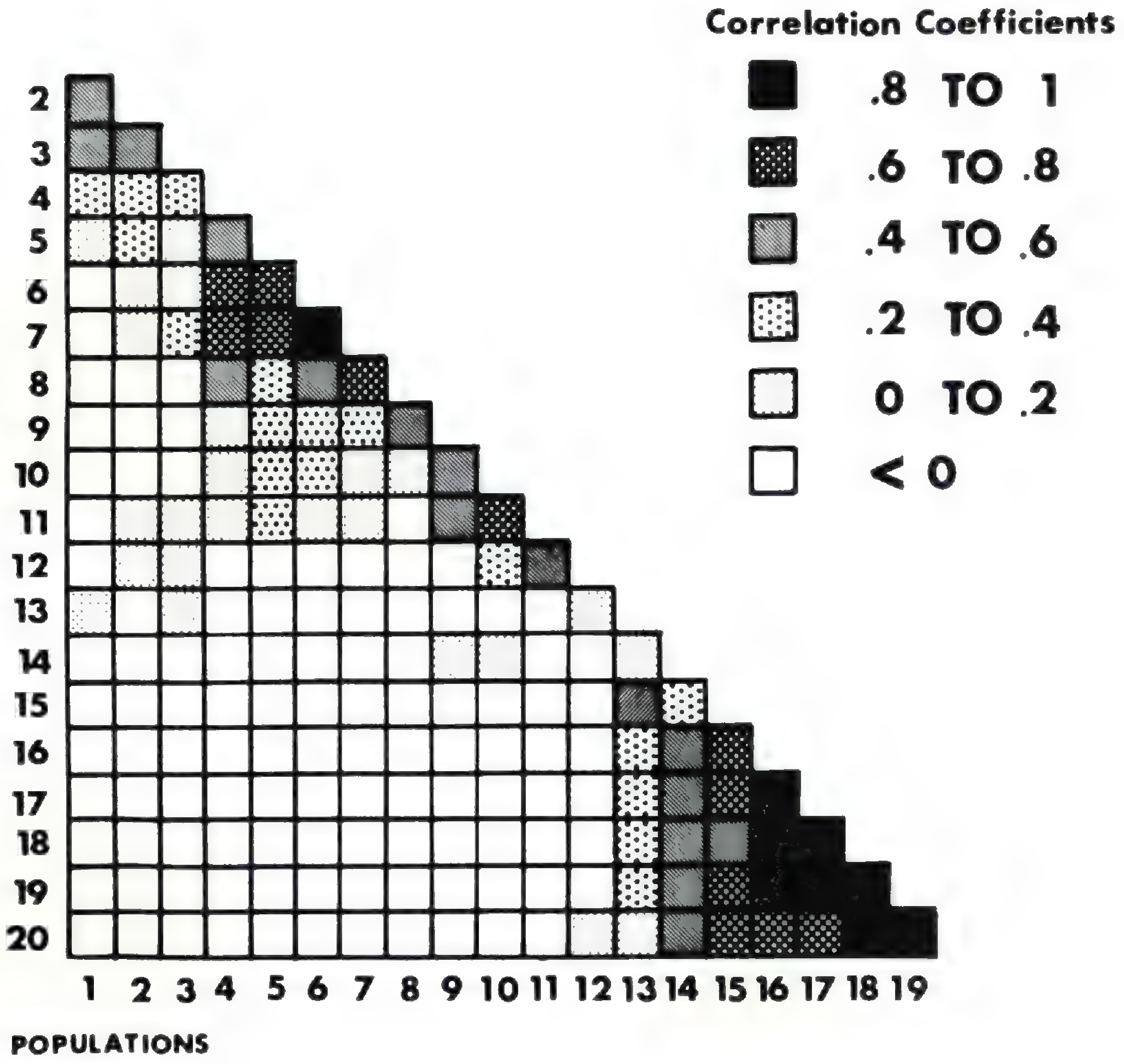


Fig. 39. Shaded correlation coefficient matrix for populations of *Cardamine bulbosa* (1-12) and *C. douglassii* (13-20). Significant correlation (0.05) equals 0.355.

Plants from community number two have previously been classified as *C. bulbosa* forma *fontinalis* (Palmer & Steyermark, 1938).

The hybrid index (Table 13, Fig. 41) indicates that with the exception of populations 12 and 13 (the Bowling Green, Ohio populations) the two species are completely separate (Figs. 41, 42). The morphologic and phenologic characters separating the species, however, break down in populations 12 and 13 (Figs. 41, 43).

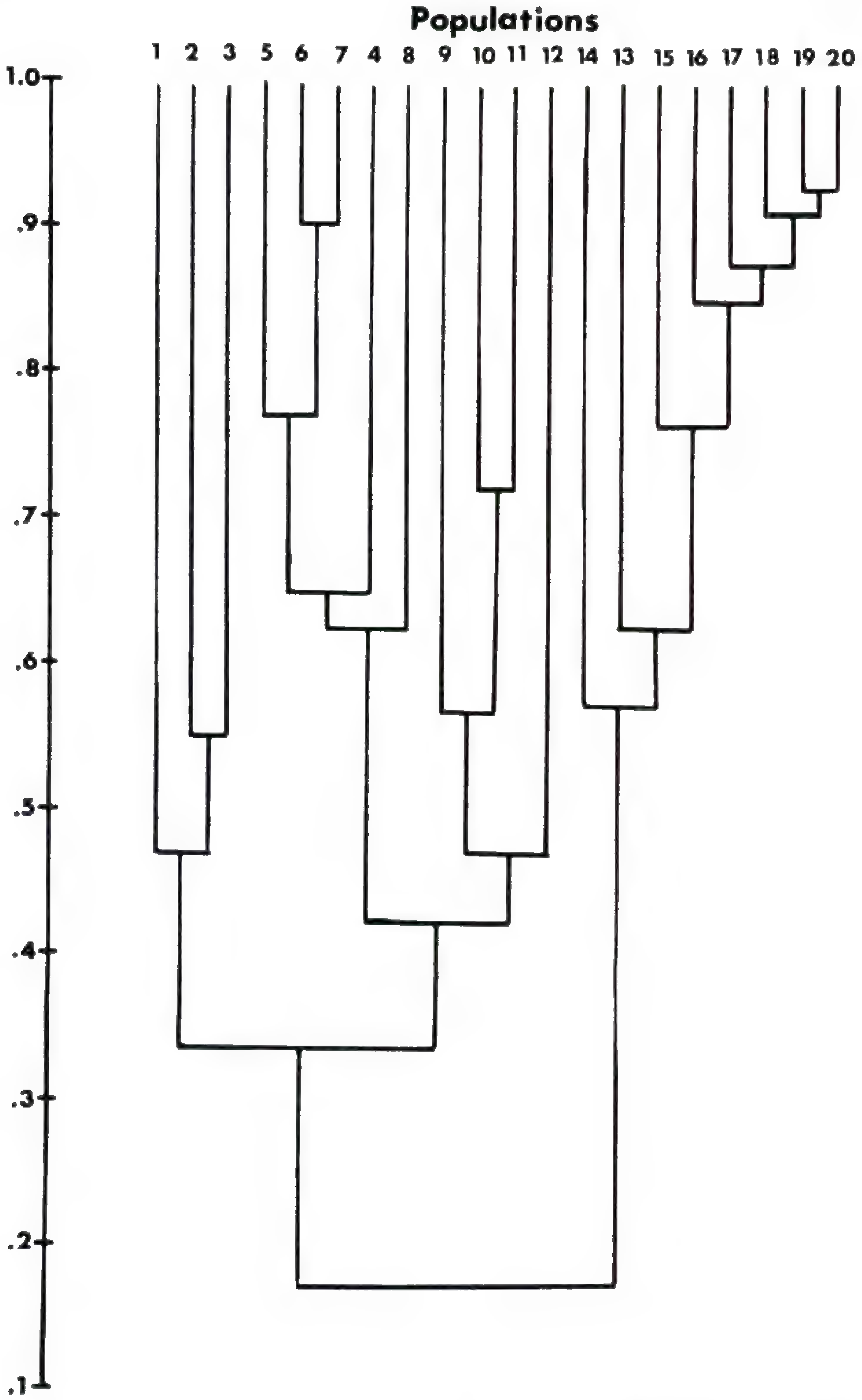


Fig. 40. Correlation phenogram of populations of *Cardamine bulbosa* (1-12) and *C. douglassii* (13-20) with clustering based upon the highest mutual correlation. Significant correlation (0.05) equals 0.355.

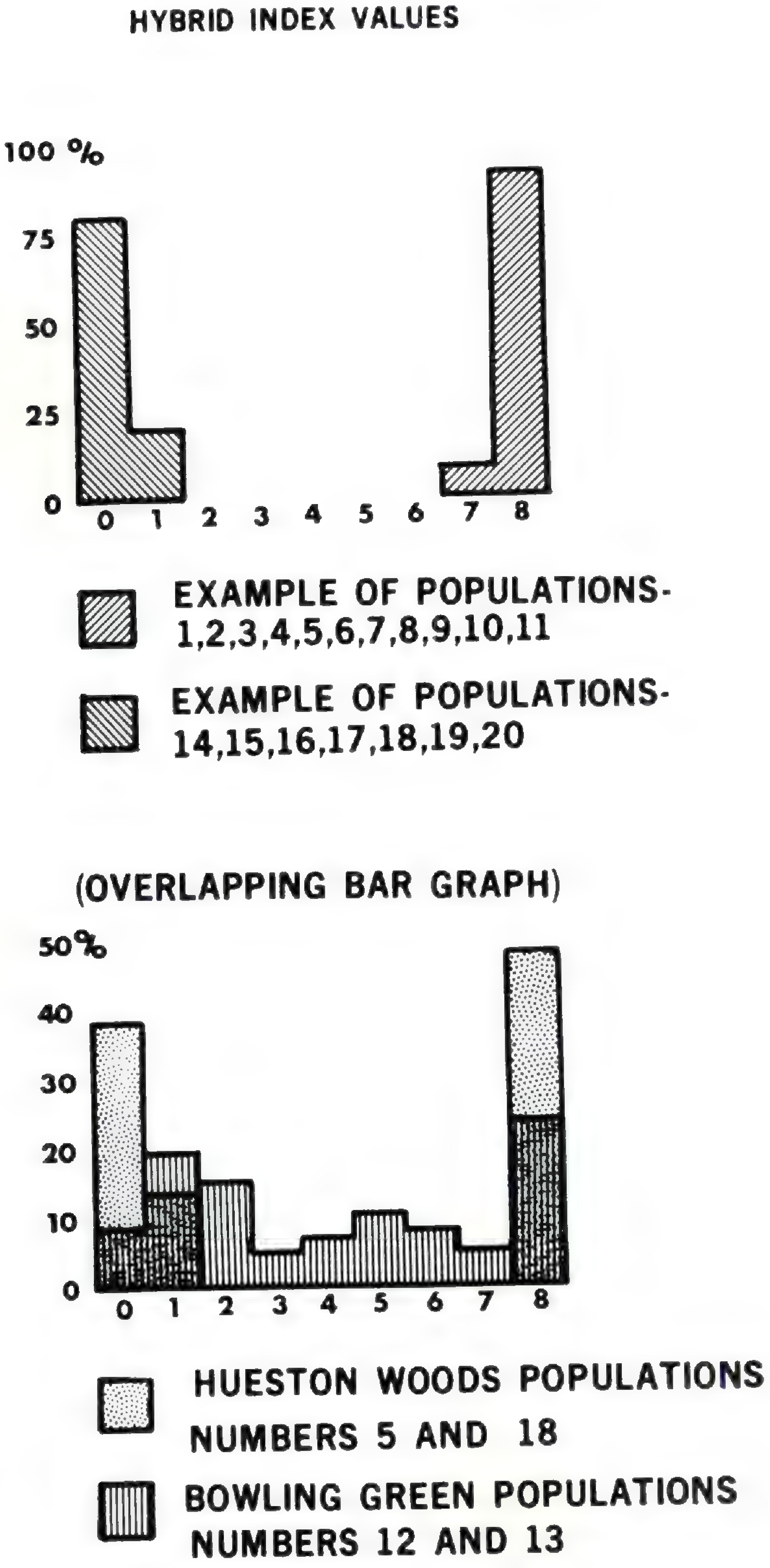


Fig. 41. Hybrid index values of typical populations of *Cardamine bulbosa* (1-12) and *C. douglassii* (13-20) as well as a hybrid swarm from Bowling Green, Ohio.

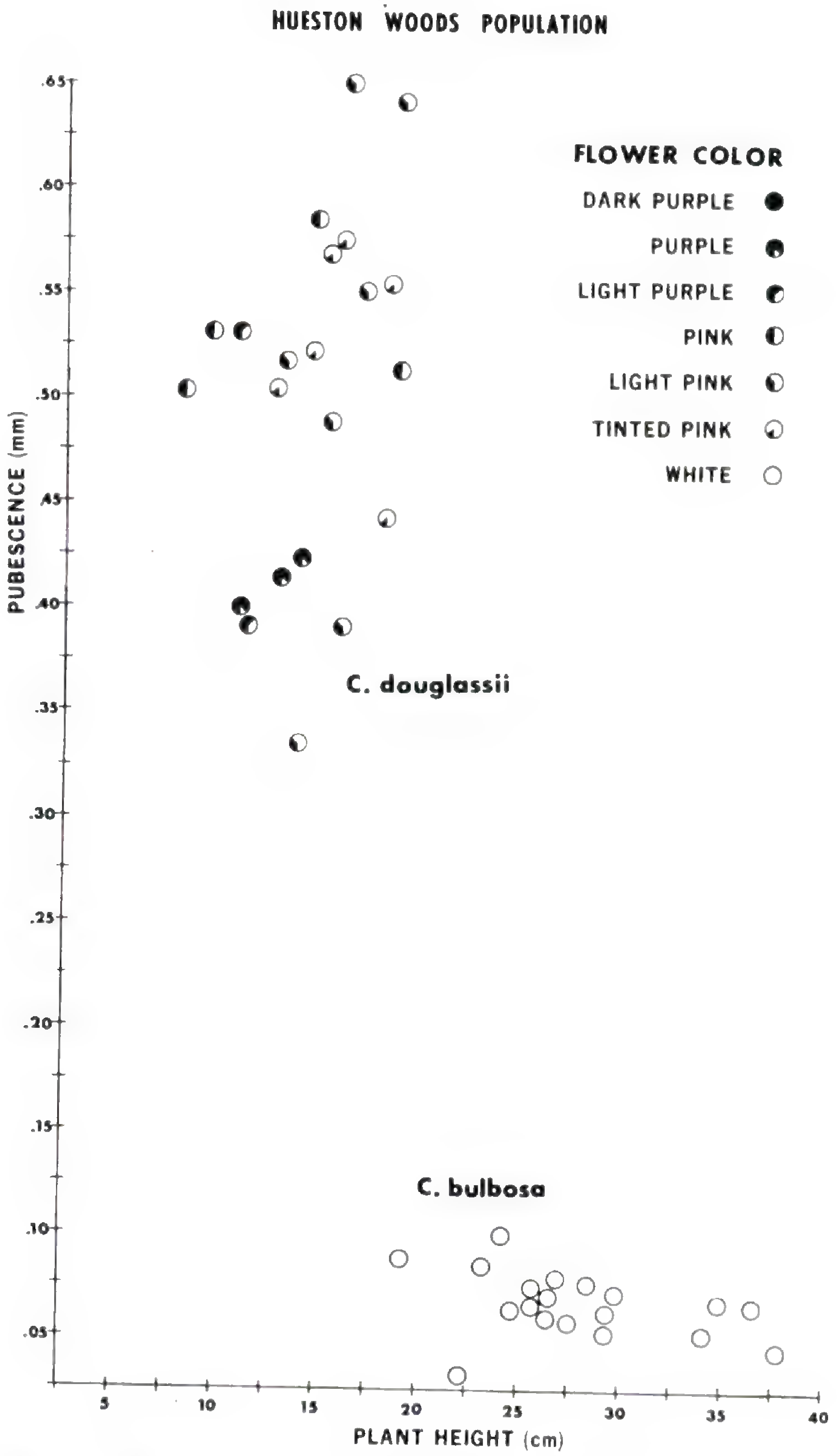


Fig. 42. Scatter diagram depicting the relationship of *Cardamine bulbosa* and *C. douglassii* from the Hueston Woods populations (Nos. 5 and 18).

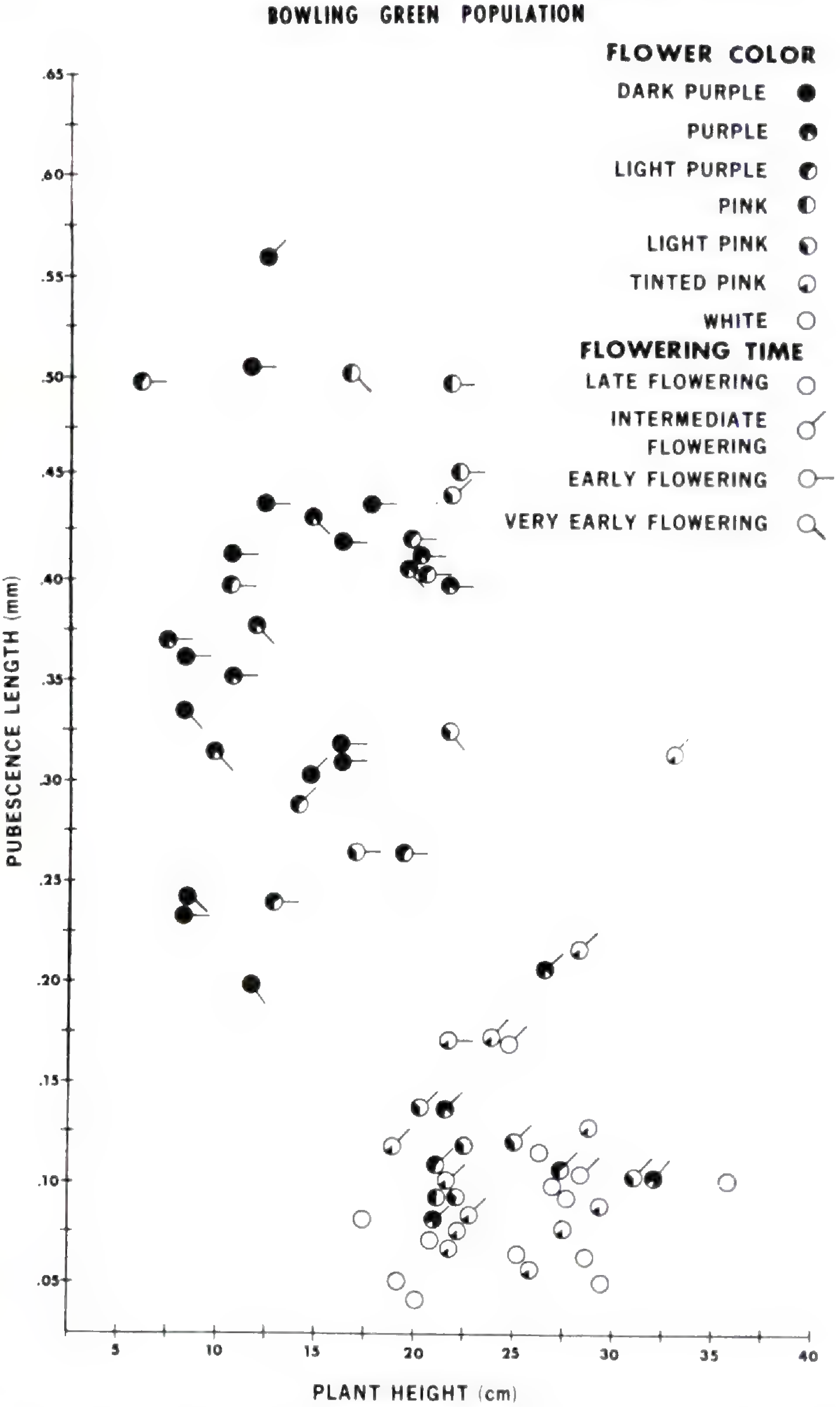


Fig. 43. Scatter diagram depicting the relationship of *Cardamine bulbosa* and *C. douglassii* from the Bowling Green populations (Nos. 12 and 13).

TABLE 13. HYBRID INDEX PERCENTAGES OF POPULATIONS OF *CARDAMINE BULBOSA* AND *C. DOUGLASSII*

Population	Hybrid			Index			Percentages		
	0	1	2	3	4	5	6	7	8
1	—	—	—	—	—	—	—	17	83
2	—	—	—	—	—	—	—	13	87
3	—	—	—	—	—	—	—	15	85
4	—	—	—	—	—	—	—	—	100
5	—	—	—	—	—	—	—	—	100
6	—	—	—	—	—	—	—	—	100
7	—	—	—	—	—	—	—	18	82
8	—	—	—	—	—	—	—	38	62
9	—	—	—	—	—	—	—	10	90
10	—	—	—	—	—	—	—	—	100
11	—	—	—	—	—	—	—	8	92
12, 13	8	19	15	5	7	11	8	5	23
14	53	47	—	—	—	—	—	—	—
15	93	7	—	—	—	—	—	—	—
16	60	40	—	—	—	—	—	—	—
17	80	20	—	—	—	—	—	—	—
18	72	28	—	—	—	—	—	—	—
19	78	22	—	—	—	—	—	—	—
20	67	33	—	—	—	—	—	—	—

Morphologically the best diagnostic characters for separating *Cardamine bulbosa* from *C. douglassii* (Figs. 44, 45, 46) are pubescence length (Fig. 30), plant height (Fig. 31) and flower color (Fig. 35).

There is no overlap in pubescence length between the two species under normal conditions. *Cardamine bulbosa* normally has hairs less than .15 mm long while normal *C. douglassii* has hair lengths greater than .2 mm (Fig. 34). Problems do arise in that plants with hair lengths falling between .12 and .25 mm do occur (Figs. 34b, 43). These plants often are intermediate in other characters such as flowering time, flower color, and plant height. Throughout this study, those plants with intermediate hair length and flowering time have been considered to be putative hybrids.

Putative hybrids between the two species appear to be relatively rare; however, a few have been found at the John Bachelor Preserve (pop. 19) near Oxford, Ohio, and one at Camp Hook (pop. 14) near Franklin, Ohio. Large numbers of putative hybrids (Fig. 47) were found near Bowling Green, Ohio (populations 12 and 13).

Cardamine douglassii plants at the Bowling Green location (population 13) are somewhat different from most of the other populations of *C. douglassii* studied. They are somewhat like *C. bulbosa* in that the pubescence is shorter and the plants are taller than most *C. douglassii* populations. Bowling Green *C. douglassii* also have a greater petal index and length than do most of this species.

In this same location *Cardamine bulbosa* is found interspersed among the *C. douglassii* plants (Fig. 47). The plants of *C. bulbosa* at this locality have very large petals, many of which tend to be pinkish in color. This may be an indication of introgression or heterosis due to hybridization. In addition these plants have longer pubescence and fewer cauline leaves than most populations of *C. bulbosa*. These species are growing intermixed in this location and each is revealed to be different from other populations of the same species. These aforementioned factors and the presence of large numbers of putative hybrids (Figs. 41, 43) at this locality are strong indications of relatively large amounts of past or present gene flow between the two species in this community.

Dr. John Beaman, Michigan State University (personal communication) reported that *Cardamine bulbosa* and *C. douglassii* differ in their leaf index. This possibility was investigated and could not be substantiated for the plants studied (Table 11, char. 18). However, a correlation between leaf index of the first leaf and pubescence length and petal color was discovered. A comparison of populations 12 and 13 with other *C. bulbosa* and *C. douglassii* populations suggests the presence of introgressive hybridization in the Bowling Green, Ohio population (Heiser, 1973).

Figs. 44-47. Fig. 44. Habitat photo of *Cardamine bulbosa,* Chemical race A. Fig. 45. Habitat photo of *C. bulbosa,* Chemical race C. Note the many branches. Fig. 46. Habitat photo of *C. douglassii.* Fig. 47. Habitat photo of Bowling Green, Ohio populations (12 and 13). *Cardamine douglassii* is on the left, *C. bulbosa* on the right, with a putative hybrid in the center.

A previous report of the petal size of *Cardamine douglassii* exceeding that of *C. bulbosa* (Stuckey, 1962) does not appear valid. The three largest petal averages were found in *C. bulbosa* (Table 11). The largest petals were found in populations of *C. bulbosa* high in water content with the exception of the Bowling Green population (no. 12). While not statistically significant, it is interesting to note that four of the five populations having the smallest petals are found within *C. bulbosa* having numerous branches.

Stuckey (1962) mentioned the possibility that *Cardamine bulbosa* (Muhl.) B.S.P. var. *hirsuta* O. E. Schulz was similar to some of the pubescent forms from southwestern Ohio. He may have been referring to certain plants of a race characterized by: numerous branches, the chemical race C pattern, numerous stem hairs, short hairs and smaller flowers with a tendency to have pinkish petals. Numerous branches occur in this race of *C. bulbosa* but not in the species as a whole (Figs. 44, 45). Therefore, this character should not be used as a diagnostic species characteristic, as has been done previously.

Leaf index is correlated with chromosome number in both *Cardamine bulbosa* and *C. douglassii*. However, one cannot tell the chromosome number of a plant by examination of the leaf index due to the overlap involved.

POPULATION FITNESS

An intriguing method for the measurement of the degree of fitness and the homogeneity of populations in their respective environment was presented by Davidson and Dunn (1967). Their method expects a high variability (many uncorrelated factors) in an undisturbed or ancestral situation. They assume that in an environment favorable to the growth of the species there will be more plant to plant variability than in a marginal environment.

The Davidson and Dunn (1967) model imagines species X as being comprised of a number of biotypes (different

genetic combinations) which occupy an environment at a given point in time. The biotypes that are most fit in that environment are likely to contribute the greatest number of genes to the subsequent generation. As selection will tend to reduce the potential variability contained in the biotypes, those biotypes most fit or best adapted to the environment can be thought of as having the potential for higher variability and as having reached an adaptive peak in that particular environment.

If elements of Species X invade a peripheral or ecologically new environment, they may produce a founder population (Mayr, 1942) effectively isolated from other members of the species. Davidson and Dunn (1967) have proposed that: 1) The number of genes incorporated into the new population will be directly proportional to the number which originally entered the population and 2) inversely proportional to the amount of selection pressure for fitness. The number of genes in the founder population is likely to be less than in the original populations, because fewer genes are likely to be introduced, and the selection pressures will probably be different in the new environment. The exact genes contributing to the founder population will depend on which genes entered the populations, the amount of selection, and upon the particular gene(s) affected by selective pressures peculiar to the new environment. Only a portion of the parental genes are introduced and the new population is exposed to different environmental pressures. It is unlikely, therefore, that the new adaptive peak of the founder population will be the same as the parent population.

They conclude that the genetic make-up of the founder population will be different and more homogeneous or less variable than in the original population. This is in agreement with Mayr (1963) who refers to the founder principle saying that "total genetic variation tends to decrease as local populations encounter presumably new selective forces in environments and habitats other than those occupied earlier by predecessor populations."

The founding population, in time, may become more variable through genetic changes. The rate of recovery will depend on the number of sets and kinds of genes which are found in the population as well as time, chance, and the amount of selection against the mutants and recombinants. This polygene recovery may be rapid at times.

The genetic variation may also be considered to vary depending on the environmental features influencing the various characters. Studies treating environmental features as independent variables and morphological characters as dependent variables are relatively common (Hopkins, 1938; Epling & Dobzhansky, 1942; Brown, 1957; Birch *et al.*, 1963). These studies indicate many linear relations between specific environmental and various populational features.

It is usually assumed that genetically different migrants invade selectively different habitats, and changes under these differing conditions are unique in each. Selection by one environment may directly affect genes while under a different environmental selection different genes may be affected.

As a means of measuring the differences between the genetic variability of different populations caused both by evolutionary history (founders principle) and environmental selection, Davidson and Dunn (1967) recommend the use of the correlation coefficient. Upon making random samples, assuming equal variances for the characters, the correlation coefficient is a measure of how close the characters come to having a linear relationship with each other.

It is assumed that the greater the number of correlated characters or the less plant to plant variability they exhibit, the younger the population and/or the higher the selection pressure that plants in this population are under.

Nineteen populations were included in this study with fifteen to twenty plants per population being studied. The population from Pulltight Springs, Missouri, was not included due to the lack of sufficient specimens. Twenty characters were used (Hart, 1972, Appendix 15). These

particular characters were studied since many are important species characters and they appear to be normally distributed.

Difficulties were encountered with plants from the Bowling Green population since some could not be positively identified to species due to the hybridization occurring in this area. Only specimens considered to be pure were used in this test. Had the putative hybrids and backcrosses progeny been included, the variability of both species might have been increased.

A program using the APL/360 computer first standardized all characters and then computed the correlation coefficients (Hart, 1972, Appendix 3). The degrees freedom used were (n — 2) with n equalling the lowest number of measurements used in the computation of the correlation coefficients. Thirteen degrees of freedom were used as the smallest number of plants studied in the populations included here was fifteen.

A measure of within-population correlation magnitude was calculated using the i coefficient of Davidson and Dunn (1967).

The Davidson and Dunn coefficients (Table 14) for pure populations of *Cardamine douglassii* and *C. bulbosa* are similar with both the highest and lowest coefficients found in populations of *C. bulbosa.* As the i values of the populations of *C. douglassii* tend to be slightly higher than those of *C. bulbosa,* one might suspect *C. douglassii* to be the derived species. The different chromatographic patterns of *C. bulbosa* have variable i values, thus failing to indicate which of the races is younger.

The Davidson and Dunn method indicates that *Cardamine douglassii* is the derived species, although no definite conclusions can be reached in this example with reference to the founders principle. The intraspecific variation noticed may be due mostly to environmental selection. *Cardamine douglassii* has three populations with relatively high i values. The Bowling Green population where hybrids are common is intermediate in its i value. If a breakdown of

TABLE 14. INTRAPOPULATION VARIABILITY USING THE DAVIDSON AND DUNN i VALUE

Population Number	Chromosome Number	Chemical Race	Average percent water	i value DF = 13
Cardamine douglassii				
14	32	A	87	26
16	32	A	51	26
15	48, 72	A	84	32
13	48	A	100	37
18	32	A	60	37
19	32	A	33	39
20	32	A	57	40
17	—	A	71.8	53
Cardamine bulbosa				
4	32	C	100	14
5	32	A	60	17
12	32	A	100	22
6	32	C	100	24
9	32	A	100	24
7	32	C	67	25
3	—	A	100	31
1	48	A	100	37
8	32	C	100	43
11	—	—	100	48
10	48	—	46	59

the species themselves is occurring in this location, one might expect much higher variability than is indicated by the i value.

Water has commonly been thought to be an important factor separating these two species (Stuckey, 1962; Gleason & Cronquist, 1963) and it should be noted that in the Bowling Green (no. 13) population the soil is extremely wet, possibly too wet for high variability of *Cardamine douglassii*. The population at the John Bachelor Preserve (no. 19) exhibits the reverse situation with the presence of a sandy soil which may be too dry for this species. The Rush Run population (no. 17) is located in a highly disturbed, moist upland woods. All populations with a high i value differ from most other populations of *C. doug-*

lassii by being either unusually wet, dry or in a disturbed community.

One population of *Cardamine bulbosa* located near Ugly Creek in Mammoth Cave National Park is much less variable than the others. This population appears to be under high selection pressure causing the variables to be highly correlated. The soil is quite dry for *C. bulbosa* and ecologically the area appears more typical of one inhabited by *C. douglassii*.

SPECIES DISCUSSION

Cardamine bulbosa is an extremely variable species in comparison to *C. douglassii*. This may be seen morphologically through the use of correlation and distance coefficients and with the Davidson and Dunn (1967) i value. It has also been shown that both chemically and ecologically *C. douglassii* is much less variable than *C. bulbosa*. If the assumption of an increase in variability through time is correct, *C. douglassii* is probably derived from the widespread *C. bulbosa*.

Three chemical races of *Cardamine bulbosa* were found. *Cardamine bulbosa* forma *fontinalis*, found growing almost submerged in cold spring water, possesses one of the distinctive chromatographic patterns (Race B). The other two chemical races do not differ ecologically. However, one (Race C) normally has more branches and tends to have white to slightly pink flowers and a large amount of pubescence. Race A normally has few, if any, branches, and white flowers with only a small amount of short pubescence. Stuckey (1962) considered naming the varieties he found which differed as to the amount of sepal pubescence. His pubescent variety appears to be equivalent to chemical race C. Populations of this chemical race can be identified morphologically; however, identification of many individual specimens without chromatograming is questionable. Based on the numerous branches and hairs it would appear that the type specimen (Type *Clayton s. n.* BM, ex. Herb. Gronovii) of *C. bulbosa* belongs to chemical race C.

In *Cardamine bulbosa,* chemical race C possessing quercetin and chemical race A hybridize easily under greenhouse conditions. It is also quite difficult to tell some of these individuals apart based on external morphological characters. Further investigation into the genetics and geographic distribution of the chromatographic patterns may indicate the biological and evolutionary importance of the different patterns and their associated morphological characters. If further research indicates that *C. bulbosa* — chemical race A tends to be similar in range to *C. douglassii,* then a close look at the morphology of *C. douglassii* and the various races of *C. bulbosa* will be necessary. In number of branches, petal length, as well as the chromatographic pattern itself, *C. bulbosa* — chemical race A is more similar to *C. douglassii* than it is to *C. bulbosa* — chemical race C. The possibility that *C. bulbosa* — chemical race A is a variety of *C. bulbosa* possessing some genetic material from *C. douglassii* should not be overlooked in further investigations.

The evolutionary significance and the geographic distribution of polyploidy within *Cardamine bulbosa* and *C. douglassii* is poorly understood. The presence of the chromosome number of $n = 48$ in the two northern populations of *C. douglassii* studied may be explained by the fusion of a normal haploid egg ($n = 32$) with an unreduced diploid sperm. The fact that some plants with haploid numbers of 72 in addition to plants with $n = 48$ were found in population 15 at Bedford, Ohio, lends further support to this hypothesis.

Low intrapopulational variability, as indicated by high Davidson and Dunn i values, is found in ecologically borderline habitats of both species. The highest i values were found in a very dry community containing *C. bulbosa* and a wet, disturbed community containing *C. douglassii.*

The logic of recognizing two species, *Cardamine bulbosa* and *C. douglassii,* was previously questioned by Schulz (1903). On the other hand, most modern authors have recognized these taxa as two species.

Before resolving this conflict, one must define his own species concept. Mayr's (1969) biological species definition states that "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups." Many botanists prefer different species to have a "certain degree" of morphological difference in addition to reproductive isolation. This is due, in part, to the presence of polyploidy and apomixis in plants, as well as the opinion of some that a classification should be useful to the herbarium or classical taxonomist.

Isolation of the genomes is extremely important in the development of biological species. Assume, for instance, that *Cardamine bulbosa* contains genes which help adapt the species to one particular niche. These particular genes are present in the individual breeding population because of selection by the environment. A second breeding population (*C. douglassii*) in a different ecological niche but in the same community as the first is exposed to different selective forces and would contain different arrays of co-adapted genes.

Crossing between members of the different populations will produce many untested presumably poorly adapted genotypes. If the parental populations differ with respect to an adaptive gene combination of ten or more independent genes, over 99.9% of their F_2 zygotes could be expected to be subvital recombinations (Grant, 1971).

This huge loss of reproductive potential resulting from interbreeding of differentiated sympatric populations can be contrasted with the generally beneficial results of interbreeding within the same population. In this situation blocks to hybridization would be favored by natural selection and would spread through each of the populations (Grant, 1971; Wallace, 1968).

A stable biotic community is composed of reproductively isolated breeding populations. Sexual reproduction between members of different breeding populations would lead to the breakup of adaptive gene combinations within each population. A biological species, then, is composed of breed-

ing populations reproductively isolated in nature. This reproductive isolation must be somewhat complete in order to prevent the breakup of beneficial gene combinations. The isolation mechanisms necessary for two lines to evolve separately may be internal or external and need not act under laboratory conditions or in artificial cross pollinations.

Sokal and Crovello (1970) conclude that the biological species definition will not apply equally to both the classical species (morphological) and the evolutionary species. Furthermore, in effect, two or three species definitions may be required.

The particular species definition used in any one group of plants may depend in part on the plants themselves as well as the background or emphasis of the particular taxonomist. Grant (1963, 1971) and Cain (1954) recognize the importance and need of distinguishing between the biological species and the taxonomic species. The biological species definition emphasizes reproductive isolation while the taxonomic species definition emphasizes phenetic or morphologic variation. Both are commonly related to each other; however, many problems arise from sibling species, polyploidy and apomixis.

An emphasis on evolution instead of reproduction or morphology necessitates a third species definition, that of the evolutionary species (Grant, 1971). The evolutionary species is a group of populations which are 1) an ancestral-descendant sequence of populations, 2) evolving separately from other such lineages, 3) fitting their own particular ecological niche in a biotic community, 4) susceptible to change in their evolutionary role through time (Simpson, 1961).

Much of the argument over species definition appears to depend on the background of the taxonomist. At times it may be necessary to discuss the classification of a population of plants from these three viewpoints — biological, taxonomic, and evolutionary. "Viewed from the standpoint of the evolutionary species concept, however, the

important question is not whether two species hybridize, but whether two hybridizing species do or do not lose their distinct ecological and evolutionary roles. If, despite some hybridization, they do not merge, then they remain separate species in the evolutionary perspective" (Simpson, 1961).

Considering the total biology of *Cardamine bulbosa* and *C. douglassii* permits a better understanding of the species problem in these two taxa. In the study of *C. bulbosa* and *C. douglassii,* artificial hybrids were produced with relative ease in the greenhouse. In addition, natural putative hybrids were found in three different areas in Ohio. Since these two taxa are not completely reproductively isolated, they cannot be considered as different biological species.

The status of *Cardamine bulbosa* and *C. douglassii* as a taxonomic species is dependent on the amount of morphological difference one equates with species differences. The data previously presented indicate that both taxa can always be separated on pubescence length assuming little or no hybridization is occurring in the population. Other good characters separating the taxa are: flowering time, habitat, flower color, height, and time of meiosis. Taking into account both the morphological and physiological characters studied, one can always differentiate between so-called good *C. bulbosa* and *C. douglassii.* As the characters separating the two species appear to be fixed and are not variable from place to place one must assume that the taxa are genetically isolated from one another. They are not completely isolated by pollinator activity, crossing behavior, phenology or ecology. However, as each of these isolation mechanisms is nearly complete, one would expect that the two species are very close to being completely isolated from one another in nature. In areas, particularly along the northern edge of their ranges, where the isolation mechanisms break down one may find hybrid swarms and introgression to *Cardamine bulbosa;* however, the evolutionary importance of this is unknown. Man has probably been instrumental in the formation of these swarms

through farming techniques and various kinds of disturbances. He has similarly kept these swarms from interacting evolutionarily by isolating one population from another. It seems, then, that one may call these two taxa good taxonomic and evolutionary species as they are separated by reasonably good morphological characters and are presently distinct evolutionarily. This does not mean that future gene flow could not cause species breakdown.

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LITERATURE CITED

BEEKS, R. M. 1955. Improvements in the squash technique for plant chromosomes. Aliso **3**: 131-133.

BIRCH, L. C., TH. DOBZHANSKY, P. O. ELLIOTT, & R. C. LEWONTIN. 1963. Relative fitness of geographic races of *Drosophila serrata*. Evolution **17**: 72-83.

BLISS, C. I. 1967. Statistics in Biology: statistical methods for research in the natural sciences. Vol. 2. McGraw-Hill, New York. 639 pp.

BONHAM-CARTER, G. F. 1967. Fortan IV program for Q-mode cluster analysis of nonquantitative data using IBM 7090/7094 computers. D. F. Merriam, editor. Computer Contributions 17. State Geological Survey. University of Kansas, Lawrence. 28 pp.

BRITTON, N. L. 1889. New or noteworthy North American phanerogams, II. Trans. N. Y. Acad. Sci. **9**: 6-15.

BROWN, W. L.. JR. 1957. Centrifugal speciation. Quart. Rev. Biol. **32**: 247-277.

BUTLER, C. G. 1945. The behavior of bees when foraging. J. Roy. Soc. Arts **93**: 501-510.

CAIN, A. J. 1954. Animal species and their evolution. Hutchinson and Co., Ltd., London. 190 pp.

CAZIER, M. A., & A. L. BACON. 1949. Introduction to quantitative systematics. Bull. Amer. Mus. Nat. Hist. **93**: 343-388.

DAVIDSON, R. A., & R. A. DUNN. 1967. A correlation approach to certain problems of population-environment relations. Amer. J. Bot. **54**: 529-538.

DEAM, C. C. 1940. Flora of Indiana. Dept. of Conservation, Div. of Forestry, Indianapolis. 1236 pp.

EASTERLY, N. W. 1963. Chromosome numbers of some northwestern Ohio Cruciferae. Castanea **28**: 39-42.

———. 1964. Distribution patterns of Ohio Cruciferae. Castanea **29**: 164-173.

———. 1965. An Illustrated Guide to the Cruciferae of Ohio. Castanea **30**: 177-191.

———. 1967. Fruit silhouettes of Ohio Cruciferae. Castanea **32**: 101-105.

EPLING, C., & TH. DOBZHANSKY. 1942. Genetics of natural populations. VI. Microgeographic races in *Linanthus parryae*. Genetics **27**: 317-332.

FARWELL, O. A. 1925. Botanical gleanings in Michigan II. Amer. Midl. Naturalist **9**: 257-282.

FASSETT, N. C. 1940. A manual of aquatic plants. McGraw-Hill Book Co., New York. 382 pp.

FERNALD, M. L. 1950. Gray's manual of botany. 8th ed. American Book Co., New York. 1632 pp.

GLEASON, H. A. 1952. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. Vol. **2**. Lancaster Press, Lancaster, Pa. 655 pp.

———, & A. CRONQUIST. 1963. Manual of vascular plants of Northeastern United States and adjacent Canada. D. Van Nostrand Co., Inc., Princeton, New Jersey. 810 pp.

GRANT, V. 1950. The flower constancy of bees. Bot. Rev. **16**: 379-398.

———. 1963. The origin of adaptations. Columbia Univ. Press, New York. 606 pp.

———. 1971. Plant speciation. Columbia Univ. Press, New York. 435 pp.

GRAY, A. 1848. A manual of the botany of the northern United States, from New England to Wisconsin and south to Ohio and Pennsylvania inclusive, . . . arranged according to the natural system, . . . James Munroe and Co., Boston and Cambridge.

GROUVILLE, A., K. EGGER, & H. PACHECO. 1970. Sur un nouveau glycoside du kaepférol, extrait de *Cardamine pratensis*. Compt. Rend. Hebd. Seances Acad. Sci., Serié C. **271**: 769-772.

HALL, A. V. 1970. A computer-based method for showing continua and communities in ecology. J. Ecol. **58**: 591-602.

HART, T. W. 1972. The generic relationships and biosystematics of *Cardamine bulbosa* (Muhl.) B.S.P. and *C. douglassii* Britt. Ph.D. Dissertation, Miami University, Oxford, Ohio. 233 pp.

HARRIMAN, N. A. 1965. The genus *Dentaria* L. (Cruciferae) in eastern North America. Ph.D. Dissertation, Vanderbilt University. 217 pp.

HEISER, C. B., JR. 1973. Introgression re-examined. Bot. Rev. **39**: 347-366.

HITCHCOCK, G. S., & P. S. STANDLEY. 1919. Flora of the District of Columbia and vicinity. Contr. U.S. Nat. Herb. **21**: 329 pp.

HOPKINS, A. D. 1938. Bioclimatics, a science of life and climate relations. U.S. Dept. Agr. Misc. Publ. 280. 188 pp.

JACKSON, M. T., & R. O. PETTY. 1971. An assessment of various synthetic indices in a transitional old-growth forest. Amer. Midl. Nat. **86**: 13-27.

JOHNSON, T. F. 1970. Investigations in the floral biology of the *Arabis holboelii* complex. Master's Degree Thesis. Univ. of Washington, Seattle. 73 pp.

KERLAN, J. T. 1965. A statistical analysis of the morphological relationships within the species *Microtus longicaudis* Merriam in Utah. Master's Degree Thesis. University of Utah. 117 pp.

KONDRA, Z. P., & R. K. DOWNEY. 1968. Pollination bags for individual florets of *Brassica*. Canad. J. Pl. Sci. **48**: 108-109.

LEWIS, W. H., H. L. STRIPLING, & R. G. ROSS. 1962. Chromosome numbers for some angiosperms of the southern United States and Mexico. Rhodora **64**: 147-161.

LÖVKVIST, B. 1956. The *Cardamine pratensis* complex. Outlines of its cytogenetics and taxonomy. Symb. Bot. Upsal. **14**(2): 131 pp.

MABRY, T. J., K. R. MARKHAM, & M. B. THOMAS. 1970. The systematic identification of flavonoids. Springer-Verlag, New York. 354 pp.

MAYR, E. 1942. Systematics and the origin of species from the viewpoint of a zoologist. Columbia Univ. Press, New York. 334 pp.

————. 1963. Animal species and evolution. Harvard Univ. Press, Cambridge. 797 pp.

————. 1969. The biological meaning of species. J. Linn. Soc., Biol. **1**: 311-320.

MITCHELL, T. B. 1960. Bees of the eastern United States. Vol. 1. North Carolina Agric. Exp. Sta. Tech. Bull. 141. 538 pp.

————. 1962. Bees of the eastern United States. Vol. 2. North Carolina Agric. Exp. Sta. Tech. Bull. 152. 557 pp.

MURLEY, M. R. 1951. Seeds of the Cruciferae of northeastern North America. Amer. Midl. Nat. **46**: 1-81.

PALMER, E. J., & J. A. STEYERMARK. 1938. New varieties and forms from Missouri. Ann. Missouri Bot. Gard. **25**: 769-773.

PIMENTEL, R. A. 1958. Taxonomic methods, their bearing on speciation. Syst. Zool. **7**: 139-156.

ROBERTSON, C. 1928. Flowers and insects. Lists of visitors of 453 flowers. Privately printed, Carlinville, Illinois.

ROLLINS, R. C. 1971. Protogyny in the Cruciferae and notes on *Arabis* and *Caulanthus*. Contr. Gray Herb. **201**: 3-10.

SCHULZ, O. E. 1903. Monographie der Gattung *Cardamine*. Bot. Jahrb. **32**: 280-623.

SEIKEL, M. K. 1962. Chromatographic methods of separation, isolation and identification of flavonoid compounds, pp. 34-69. *In* T. G. Geissman (ed.), The chemistry of flavonoid compounds. Macmillan, New York.

SIEGEL, S. 1956. Nonparametric statistics for the Behavioral Sciences. McGraw-Hill, New York. 312 pp.

SIMPSON, G. G. 1961. Principles of animal taxonomy. Columbia Univ. Press, New York. 247 pp.

SNEATH, P. H. A., & R. R. SOKAL. 1973. Numerical taxonomy, principles and practice of numerical classification. W. H. Freeman and Co., San Francisco, 573 pp.

SNOW, R. 1963. Alcoholic hydrochloric acid-carmine as a stain for chromosomes in squash preparations. Stain Technol. **38**: 9-13.

SOKAL, R. R., & T. J. CROVELLO. 1970. The biological species concept: a critical evaluation. Amer. Naturalist **104**: 127-153.

————, & F. T. ROHLF. 1969. Biometry, the principles and practice of statistics in biological research. W. H. Freeman and Co., San Francisco. 776 pp.

————, & P. H. A. SNEATH. 1963. Principles of numerical taxonomy. W. H. Freeman and Co., San Francisco, 359 pp.

STUCKEY, R. L. 1962. Characteristics and distribution of the spring cresses, *Cardamine bulbosa* and *C. douglassii* in Michigan. Michigan Bot. **1**: 27-34.

————. 1967. *Thlaspi tuberosum* Nutt., a taxonomic synonym of *Cardamine douglassii* Britt. (Cruciferae). Rhodora **69**: 460-465.

TORREY, J. A., & A. GRAY. 1838. A flora of North America. Vol. 1. Wiley and Putnam, New York. 711 pp.

Wagner, H. 1966. Flavonoid C-glycosides, pp. 309-320. *In* T. Swain (ed.), Comparative phytochemistry. Academic Press, New York.

Wallace, B. 1968. Topics in population genetics. W. W. Norton and Co., Inc., New York. 481 pp.

Woolf, C. M. 1968. Principles of biometry. D. Van Nostrand Company, Inc., Princeton, New Jersey. 359 pp.

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EFFECT OF CLIMATE, SOIL PHYSIOGRAPHY AND SEED GERMINATION ON THE DISTRIBUTION OF RIVER BIRCH (BETULA NIGRA)

JAMES L. KOEVENIG

It is generally accepted that a flowering plant's distribution is determined by: (1) a variety of biotic, edaphic, climatic, physiographic and pyric factors and the plant's physiological response to these factors; (2) its reproductive success; (3) its powers of mobility or the dispersion of sexual and asexual disseminules; and (4) its evolutionary history, including the place and time of origin and the subsequent biotic and abiotic factors (Billings, 1952; Good, 1964; Krebs, 1972; Oosting, 1958; Raup, 1951; Tivy, 1971). Although a modified Law of Limiting Factors is still considered valid, the trend in analyzing plant distribution is to consider many interacting environmental factors (Billings, 1952; Cain, 1944; Gorham, 1954; Tivy, 1971). This approach assumes that the combined influence determines distribution, although it is recognized that when the dominant factor is in full play, minor factors are less apparent. The difficulty with this approach is that it is hard to determine quantitatively the interaction of several factors and relate it to plant distribution. As a result, most analyses of plant distribution involve situations where the dominant factor is obvious or where the effect of a single factor on one aspect of the life cycle can be easily studied.

Few distributional studies deal with trees, exceptions being the role of fire in maintaining various conifer or chaparral populations (Ahlgren & Ahlgren, 1960; Cooper, 1961; Daubenmire, 1936; Garren, 1943; Hanson, 1939; Komarek, 1967; Mirov, 1967; Mueller et al., 1968; Stewart, 1951; Stoddard, 1936; Sweeney, 1956). Studies on trees are especially difficult because of the length of the life cycle and complications involved in breeding and trans-

plant experiments. Most of the studies on trees deal with commercially important trees like the pines in southeastern United States (Ahlgren & Ahlgren, 1960; Cooper, 1961; Garren, 1943; Hanson, 1939; Komarek, 1967; Stewart, 1951; Stoddard, 1936) or on species that hybridize and are involved in some aspect of speciation (Johnson, 1939; Johnsson, 1945; Mirov, 1967; Richens, 1945; Righter, 1946; Rosendahl, 1916; Smith & Nichols, 1941; Stebbins, 1950; Syrach-Larsen, 1937). One genus, mainly of trees, that has been studied intensively is *Betula.* Most of this work, however, has focused on *B. papyrifera,* which has an unusual chromosomal situation and many varieties (Brittain & Grant, 1965a, 1965b, 1967, 1968; Clausen, 1962a, 1962b, 1966; Johnsson, 1945; Rosendahl, 1916; Stebbins, 1950). Another species, *B. nigra,* the river birch, has a distribution in the United States (Koevenig, 1975) that has led to a unique analysis of controlling factors and some insight into why the northern ranges of some plants follow the Wisconsin glacial moraine boundary.

This paper presents a hypothesis on the distribution of *Betula nigra* and reports some preliminary observations supporting it.

PROCEDURE

The distribution of *Betula nigra* (Koevenig, 1975) was compared to maps of various established climatic, edaphic and physiographic factors in the United States and to distributions of other species that might be found in similar habitats and compete with *B. nigra.*

To determine if *Betula nigra* could grow in soil outside of its northernmost range, 20 seedlings were removed from river bottomland in Blackhawk, Bremmer and Fayette counties in Iowa, within *B. nigra*'s range, late in the fall of 1965. These were bare root transplanted in soil taken from similar habitats in Le Seur County, Minnesota, outside *B. nigra's* northwestern range within the Wisconsin glacial moraine. The transplants were left in the

University of Kansas greenhouse (also outside *B. nigra*'s range) where they survived and flourished until August, 1966, when the experiment was discontinued.

Field observations were made in Iowa, Minnesota and Wisconsin to determine the extent of asexual reproduction and patterns of seed distribution. Seeds collected in Wisconsin and Kansas were checked for viability using standard germination tests and 1% (w/v) aqueous solutions of 2,3,5-triphenyltetrazolium chloride (Grabe, 1961). In some germination tests fruits were soaked for 24 hours and the fruit walls and seed coats were removed. The embryos were then placed on sterile filter paper in Petri dishes at 25°C in darkness, with and without the addition of aqueous extracts from the fruit walls and seed coats. Seedlings that developed in germination tests were transplanted to soil from within and beyond the range of *Betula nigra* to determine if soil or moisture is more important during early stages of growth. These were maintained for a year.

RESULTS AND DISCUSSION

Comparison of the distribution of *Betula nigra* with maps of various climatic, edaphic and physiographic factors revealed no obvious correlation with the exception of the pattern of major south and east flowing streams and rivers in the United States (Fig. 1). *Betula nigra* has a high soil moisture requirement, especially during early stages of growth. This is supported by my field observations that this species is found only in wet areas, unless cultivated, and by attempts to grow seedlings and transplants. Failure to keep the soil moisture near field capacity resulted in wilting of the seedlings and usually death. The lack of a major stream drainage in certain parts of the Appalachian region, Louisiana, Alabama, Arkansas and Mississippi may be one reason for the lack of reports of *B. nigra* from these regions. Seasonal lack of moisture apparently explains the western limit of *B. nigra*'s range,

Fig. 1. The major stream drainage in eastern United States (Goode, 1953) superimposed over the distribution of *Betula nigra* (Koevenig, 1975).

although none of the quantitative systems proposed to relate available moisture with plant distributions precisely correlates with the western margin. The closest fit is Thornthwaite's (1948) map of average annual water surplus in the eastern United States (Fig. 2). If Daubenmire's (1956) criticism of all major systems expressing available moisture is valid, then it is surprising that the correlation is as close as it is and this can be considered strong evidence for moisture as the major limiting factor

Fig. 2. Thornthwaite's (1948) average 5 inch annual water surplus plot superimposed over the distribution of *Betula nigra* (Koevenig, 1975).

for *B. nigra*'s western boundary. Most likely, the bottom land bordering rivers to the west of *B. nigra's* western boundary does not have sufficient moisture during the entire growing season or at certain critical times to permit survival of river birch seedlings.

The limiting factor for the northern limit of *Betula nigra* might logically be temperature, insolation, or length of growing season. However, there is no obvious relationship between the northern boundary for *B. nigra* and any single mapped climatic factor such as latitude (which should be a cutoff line if insolation were limiting), average

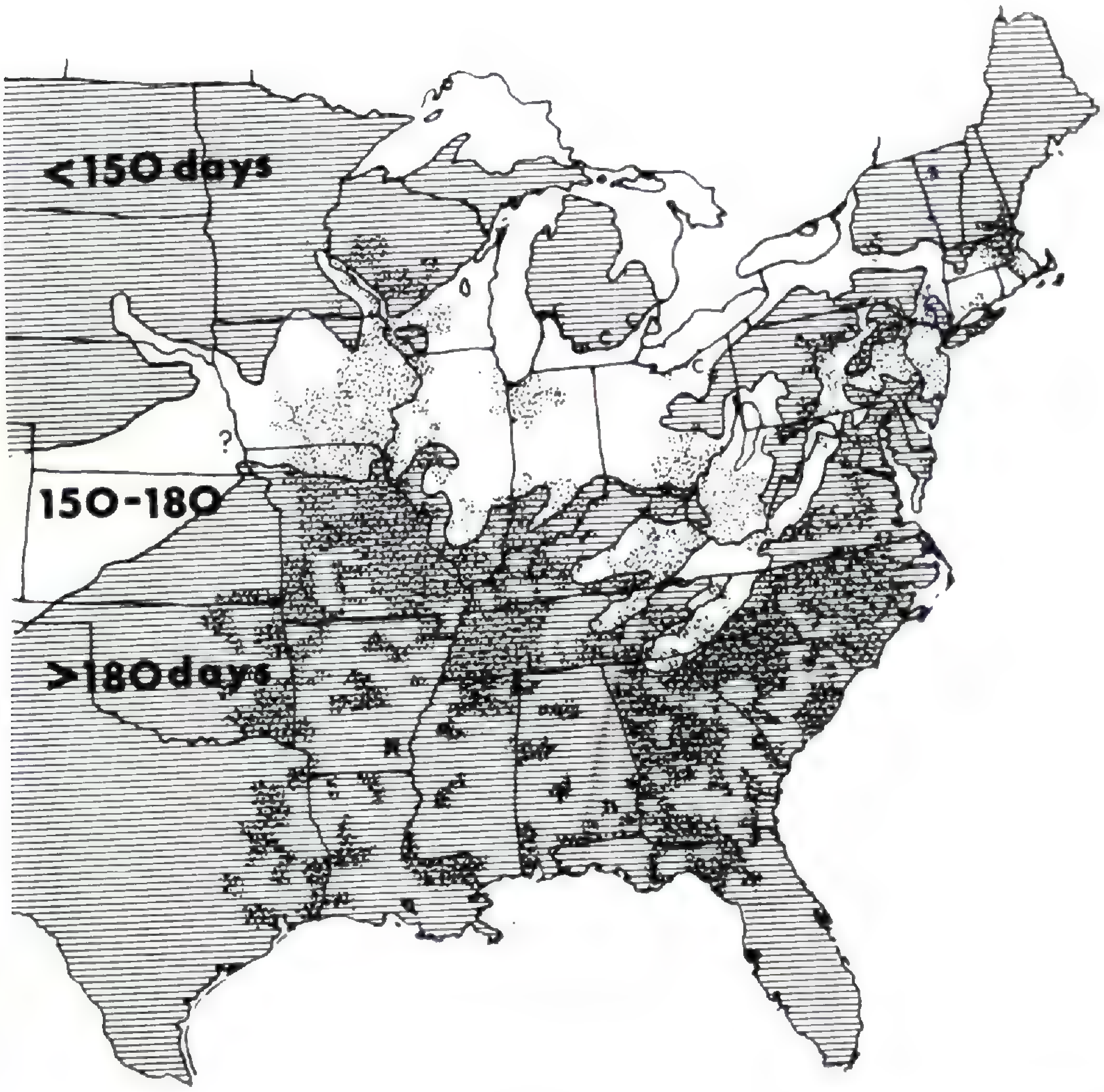

Fig. 3. Average number of days in the growing season (Goode, 1953) superimposed over the distribution of *Betula nigra* (Koevenig, 1975).

hours of daily sunshine, date of first killing frost in the fall, date of last killing frost in the spring, length of growing season (Fig. 3), average summer temperature (Fig. 4) or extreme temperatures (Goode, 1953; US Department of Agriculture, 1965). This does not mean that these factors do not play a role in determining *B. nigra*'s northern limit, especially in specific areas. Daubenmire (1956) questioned the value of considering extreme temperatures in determining the control of plant distributions. It is more likely that combinations of factors are important. In the case of *B. nigra* this is supported by some similar-

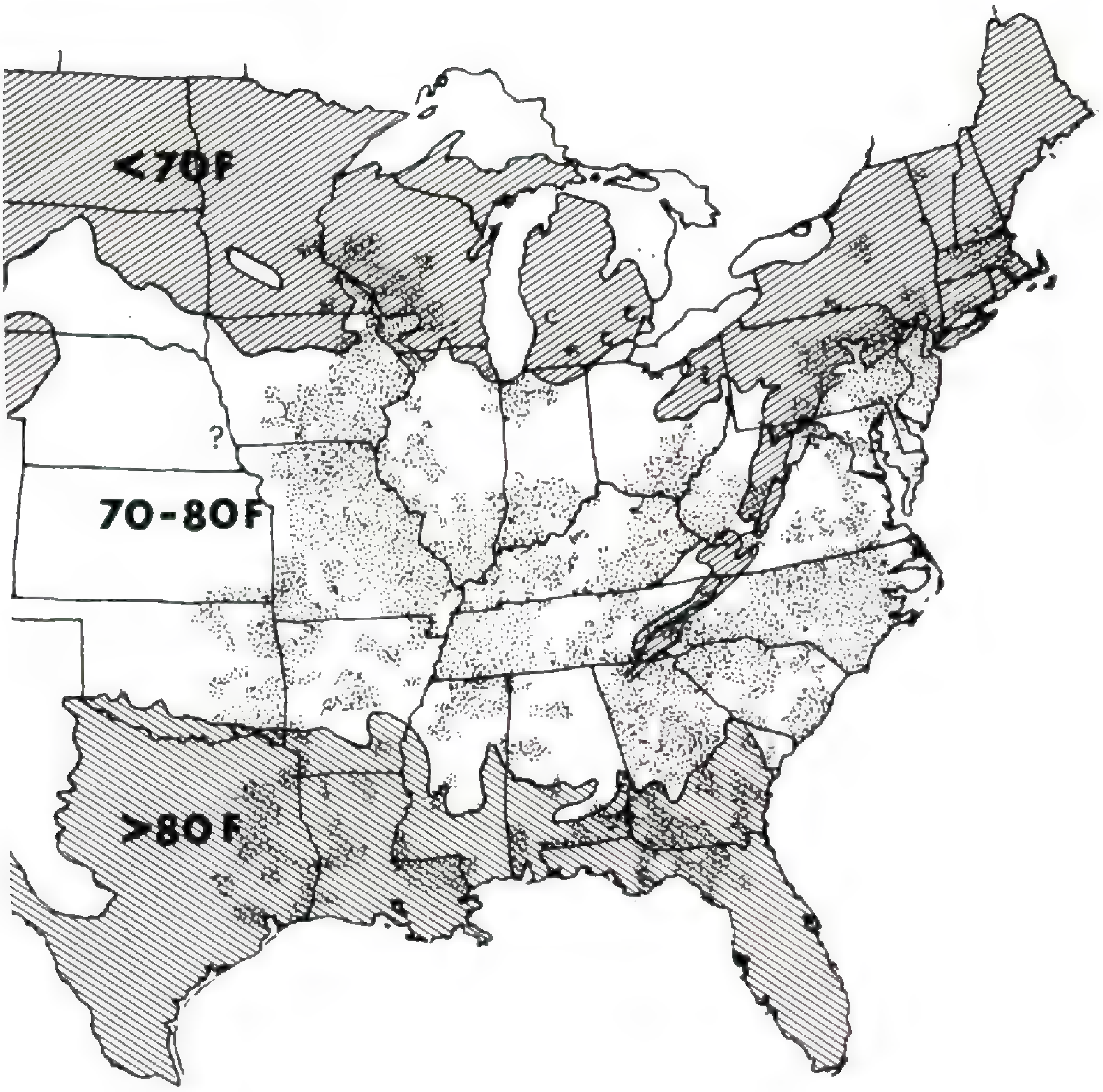

Fig. 4. Average summer temperatures (Goode, 1953) superimposed over the distribution of *Betula nigra* (Koevenig, 1975).

ity between the northern boundary of *B. nigra*'s range and Livingston's (1916) physiological-temperature index No. 6, which accounts for both temperature and moisture (Fig. 5). The persistence of plants bordering the upper Mississippi River and its tributaries, disjunct populations and cultivated plants beyond Livingston's (1916) index No. 6, or the under 70°F mean summer temperature limit (Goode, 1953), or the under 150 day growing season (Goode, 1953) suggests that some other factor(s) may be more important.

Comparison of *Betula nigra*'s distribution with various geological and physiological factors reveals a close corre-

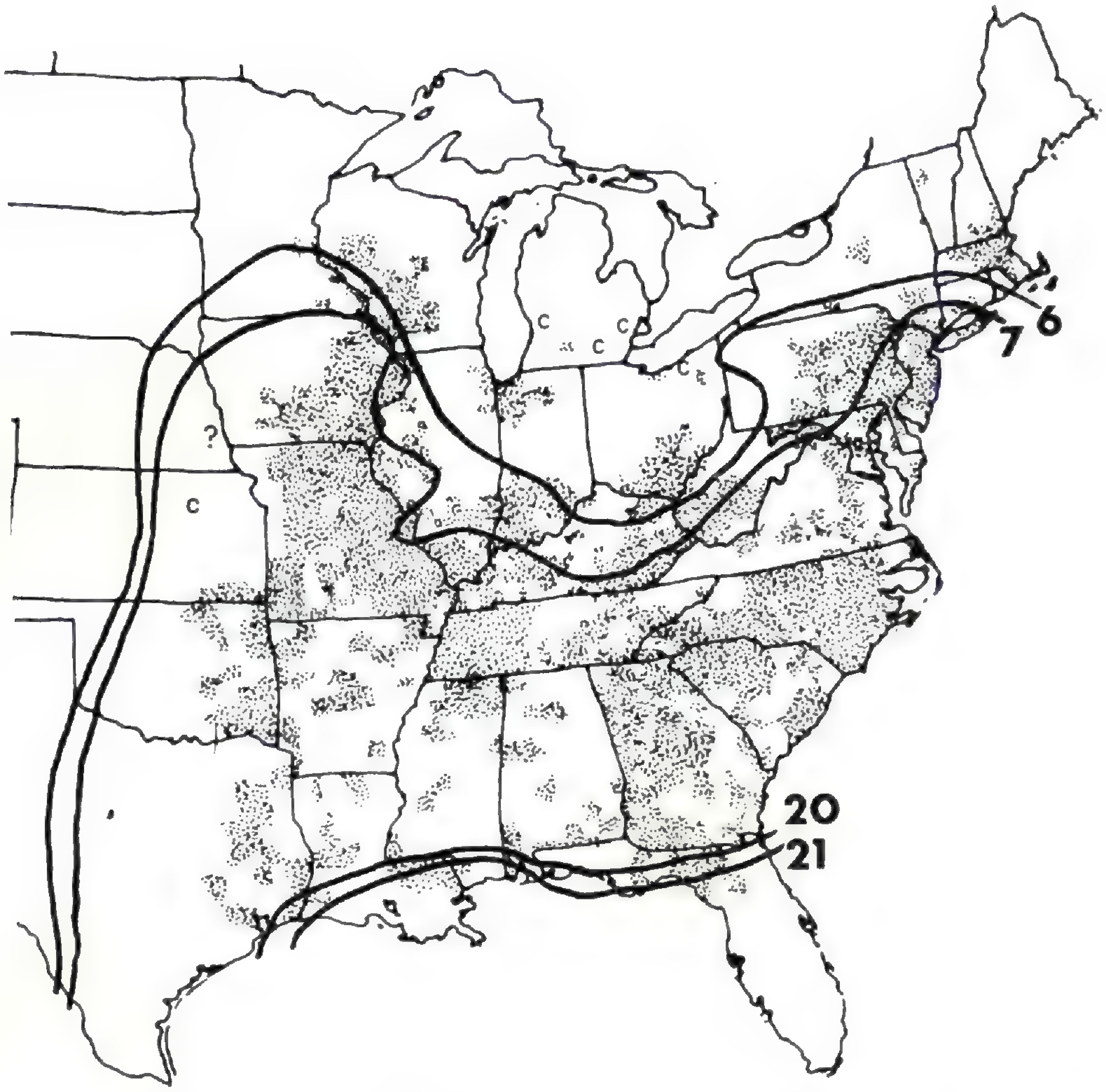

Fig. 5. Livingston's (1916) physiological-temperature indices No. 6, 7, 20 and 21 superimposed over the distribution of *Betula nigra* (Koevenig, 1975).

lation with the southern limits of the last major glacier (Koevenig, 1975). The northern limit of *B. nigra* corresponds almost exactly with the terminal moraine of the Wisconsin glacier (US Geological Survey, 1959) except around Chicago and Minneapolis and in New England. According to Braun (1955) the termination of a plant's range at or just south of the glacial border is common in the midwest and this phenomenon has attracted considerable attention (Braun, 1928, 1951, 1955; Deevey, 1949; Denny, 1951; Fernald, 1925; Gleason, 1922; Raup, 1951). Gleason (1922, p. 40) claims that the "distribution of plants . . . depends, in general terms, on modern environ-

ment and earlier developmental history. Both of these are intimately concerned with migration, the latter factor portraying its progress and the former its limitation. Neither factor alone can account completely and satisfactorily for the present range of any species." Braun (1928, 1955) offers several explanations for the termination of a species' range near a glacial boundary. All assume that the species evolved prior to the glacier. According to one explanation, the plants occupied their present range before or during the formation of the moraine, occupied it ever since and are not expanding their range at present. Two other explanations assume that when the glacier moved south it forced the plant's range southward. As the glacier receded, the plants migrated northward, but not into the former glaciated region because: (1) either there has not been enough time or (2) present climatic or edaphic conditions in this region exclude them. Gleason (1922, p. 47) proposed that the margin of a species' range "does not always represent the boundary of the territory in which the species can or will live under the present conditions, but merely the distance it has traveled so far in its march to this goal." Other possibilities not given by Braun or Gleason are that the species are prevented from moving into the moraine because of competition from plants better adapted to conditions found there, or because of some physiographic factor, or because of a combination of physiological-ecological factors.

The genus *Betula* is circumboreal and it is assumed that *B. nigra,* which is endemic to the United States, evolved prior to the Wisconsin glacier (Stebbins, 1950). This species is not considered a cold-climate plant and its northern limit was probably forced south of the glacial margin. When the glacier retreated, *B. nigra* migrated northward, but either has not had time to move into the moraine or else has been stopped there by a combination of factors.

Soil north of the moraine is younger and different in composition from soil to the south. However, *Betula nigra* occurs in bottom lands and flood plains where differences

between soil north and south of the glacial boundary are minimal. Braun (1951, 1955) ruled out the exclusion of plants from the moraine by edaphic conditions if the factors on both sides of the boundary are similar. Support for this contention comes from my transplant experiments. Seedlings and transplants both survived and grew in soil north and south of the glacial boundary. It is possible that soil differences might account for certain localized aspects of *B. nigra*'s distribution, but not for the determination of the entire northern limit.

According to observations of Stephen G. Boyce in the early 1950's (personal communication, 1973) river birch trees in southeastern Ohio grew only along streams where the pH was 5.5 or less. Based on extensive seed germination studies, he postulated that the lack of competition was a major factor. However, he did not feel his evidence was conclusive. This hypothesis seems reasonable for that specific area, but not for the entire northern limit. *Betula nigra* coexists with a variety of trees throughout its range (primarily American elm, sycamore, sweet gum and black willow in the south, cottonwood and silver maple in the east, and cottonwood and willow in the north). The species composition along any one stream is similar above and below the glacial boundary, except that *B. nigra* is absent north of the boundary. It does not appear that competition is the major limiting factor for *B. nigra*'s northern limit, although competition cannot be entirely ruled out. No other birches are found in a similar habitat and there is no evidence that *B. nigra* readily hybridizes with any other species (Clausen, 1966). Raup (1951) suggests that present distributions of species cannot be understood simply by analyzing climatic, edaphic and biotic factors on either side of the glacial boundary at a point in time, but must be interpreted in the light of the history and inheritance of the organisms in relation to the history of the soils and land surfaces.

The Wisconsin glacier established the present drainage pattern in the eastern half of the United States. Super-

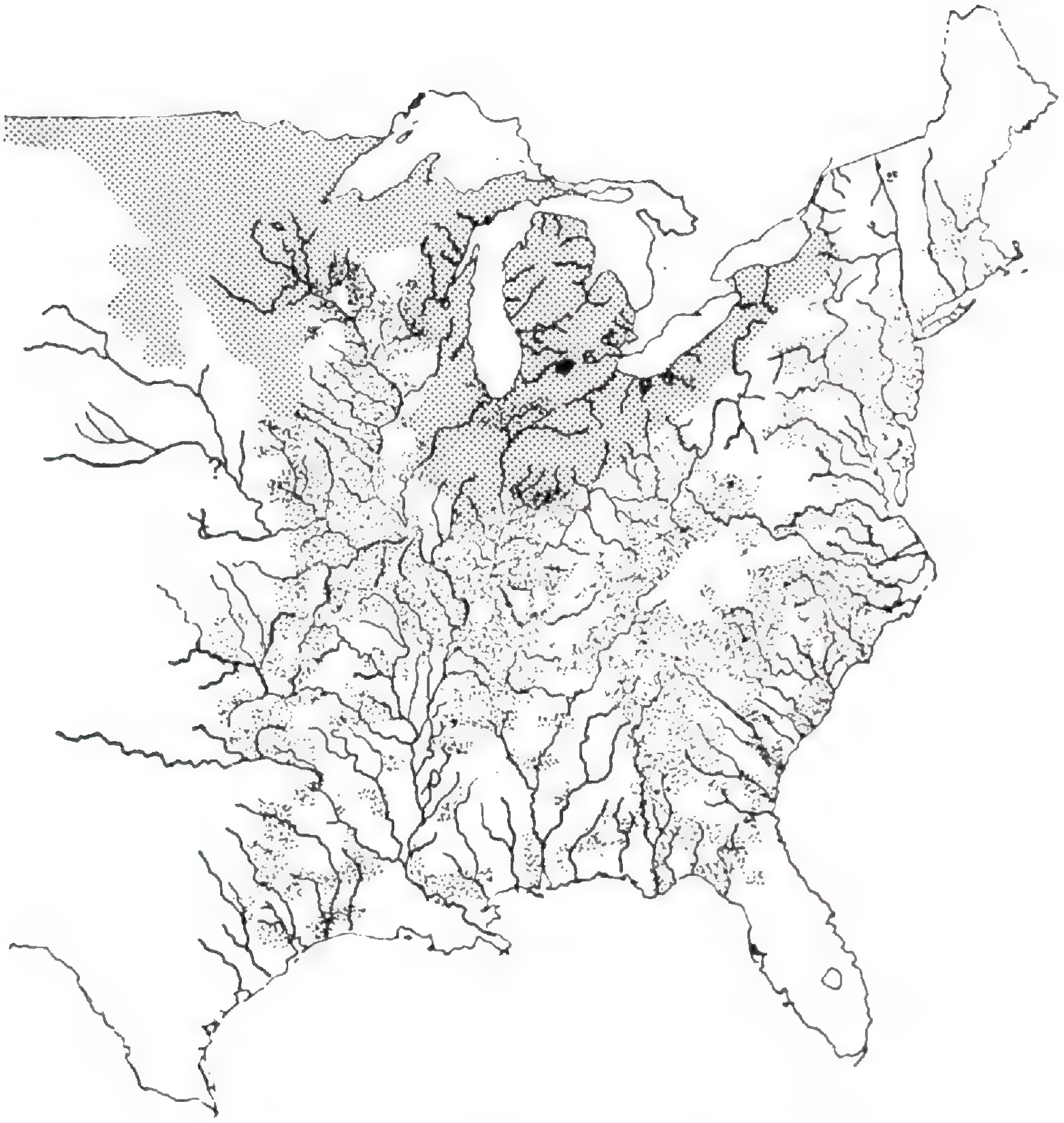

Fig. 6. The major stream drainage in the eastern United States (Goode, 1953) and the extent of the Wisconsin glacial moraine (U. S. Geological Survey, 1959) superimposed over the distribution of *Betula nigra* (Koevenig, 1975).

imposing a map of the major river system in this area over a map of the Wisconsin glacier and the distribution of *Betula nigra* (Fig. 6) reveals a close fit, except for the Illinois River, the Wabash River and their tributaries. Deevey (1949) and Gleason (1922) proposed that river drainages served as migration routes for organisms forced southward by glaciers. This explains in part why the northern range of *B. nigra* roughly fits the Wisconsin glacial moraine boundary, but it does not explain why

B. nigra has not migrated further up the rivers whose origins are north of the moraine boundary.

Plant migration involves the dispersal of seeds and/or vegetative propagules. Seeds are most important in *Betula nigra* migration and appear to play an important role in determining the northern limit. Thus far, my field work has not turned up any conclusive evidence of vegetative reproduction, but has shown that large numbers of viable seeds are produced. This is supported by Detwiler's (1916) observation of 19,790 three-month-old seedlings growing on a 6-foot square plot in a Mississippi River bottom land in Wisconsin. *Betula nigra* flowers in the spring and seeds are set immediately thereafter. The small seeds are enclosed in samaras which are borne in aments. The seeds (fruit) are wind dispersed in late May or early June, depending upon latitude and spring temperatures that year. This is about the same time as the annual spring flood or a little later. The samaras usually fall in the river, which carries them downstream, or on moist soil deposited by the flood. For example, Detwiler (1916) described great quantities of *B. nigra* seeds carried by the water to points remote from the parent tree. This facilitates rapid migration of plants downstream, but not upstream, an important factor in establishing the present distribution pattern.

River birch seeds germinate well immediately after dispersal, but germination declines with age. This was noted by Detwiler back in 1916. My preliminary experiments suggest the build-up of an inhibitor which can be removed by water. In one test of seed germination, 23 of 50 seeds (46%) germinated several days after the fruits were dispersed. When another 50 seeds from the same sample were tested 5 months later, none germinated. A tetrazolium chloride test on 20 additional seeds from that sample revealed that 15 (75%) were still viable. After seven months, 3 of 50 seeds (6%) germinated when they were soaked for 24 hr. and placed on moist filter paper, but when the fruit walls and seed coats were removed from 50 additional seeds that had been soaked for 24 hr., 40 (80%)

germinated. This suggested the presence of an inhibitor in either the fruit walls or seed coats. When the fruit walls and seed coats were removed from 50 more seeds and an aqueous extract of fruit walls was added to the soaked seeds on filter paper, 27 (54%) germinated. Likewise, 27 of 50 seeds germinated when the fruit walls and seed coats were removed and an aqueous seed coat extract was added to the soaked seeds. A study has been started to determine the nature of the inhibitor(s). Most likely the inhibitor(s) can be removed by running water, but this has not yet been conclusively demonstrated. It is not known whether the inhibitor(s) breaks down with time and whether the seeds remain viable from one year to the next when stored under various environmental conditions.

The existence of a seed germination inhibitor along with the timing of seed production explains in part the northern distribution of *Betula nigra*. The seeds are dispersed at about the same time as the spring floods or slightly later and germinate immediately if they are deposited on moist soil. Most of the seeds are carried downstream. Migration upstream is slow. Because the major drainage pattern in the northern part of the United States was established by the Wisconsin glacier, the streams drain away from the terminal moraine to the south. Any northward migration of [illegible] is dependent upon the timing of seed dispersal and the spring floods. The farther north *B. nigra* occurs, the [illegible] synchrony between these events. Colder temperatures delay flowering and seed set, yet the spring floods occur slightly earlier than they do farther south. Also, the [illegible] of the floods is less the farther north one goes and the flood plains are smaller. Within the glacial moraine boundary the nature of the flood plain changes. Denny [illegible] studied this in Pennsylvania and claimed that flood plains are essentially absent in headwater areas in glaciated regions. He attributed this to a deep congeliturbate with almost no bedrock outcroppings so that rainwater [illegible] through the superficial deposits rather than on top. [illegible] finally, the waters in the headwaters of streams move

faster and would carry seeds downstream. This means there is less chance river birch seeds will light on moist soil deposited upstream by spring floods. If germination does not occur immediately after dissemination, an inhibitor accumulates and the seeds will not germinate until there is enough water to remove the inhibitor or until the inhibitor breaks down. If the inhibitor breaks down over the winter and the seeds remain viable, then germination could take place the next spring. However, if the floods occur early, the temperatures might be too cold to permit germination. If this hypothesis is correct then *B. nigra* would be expected to spread rapidly in a local area where it borders a pond or occurs in a permanently wet area. According to A. R. Hodgdon (personal communication, 1960) this happened in New Hampshire over a thirty year period when he observed the species. *Betula nigra* would be expected to survive north of the Wisconsin glacial moraine when cultivated. There are reports of cultivated river birch trees north of the moraine boundary (Fig. 6 and Koevenig, 1975). The reported disjunct populations of river birch trees in Illinois, Michigan and northern Ohio may be cultivated or escapes from cultivation. One of these populations is located on a north-draining stream. It will be interesting to see if this population spreads downstream (north).

The distribution of *Betula nigra* in Florida might be explained as follows. Florida soils are mostly of marine deposition, except in the northern part where *B. nigra* is found. It is unlikely that these soils are suitable for good growth of *B. nigra*. Perhaps more important is that Florida is mainly a region of low surplus moisture and is subject to variation in precipitation, with most of the rain occurring from June through September after the seeds have set and been disseminated. Finally, many of the rivers in Florida are not south-draining, so rapid dissemination to the south would not occur.

The spotty distribution of *Betula nigra* in New England requires additional explanation. W. H. Camp (personal

communication, 1959) proposed that the disjunct stands of *B. nigra* are relicts from the post-Pleistocene xerothermic period when a number of more southerly plants moved north only to be left in small local areas as the "little ice age" took place. Long term observations are needed to determine if these relict populations are spreading up the rivers.

The lack of river birch trees at high altitudes in mountainous regions (*e.g.*, the Appalachians) is expected because of the lack of flood plains and the increased currents which would sweep the seeds downstream.

Further study of seed germination and viability and of the effect of temperature, biotic factors and edaphic factors on seed germination and seedling growth is necessary to shed additional light on the distribution of *Betula nigra* and the flood-seed germination hypothesis.

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LITERATURE CITED

AHLGREN, I. F. & C. E. AHLGREN. 1960. Ecological effects of forest fires. Bot. Rev. **26**:483-533.

BILLINGS, W. D. 1952. The environmental complex in relation to plant growth and distribution. Quart. Rev. Biol. **27**:251-265.

BRAUN, E. L. 1928. Glacial and post-glacial plant migrations indicated by relict colonies of southern Ohio. Ecology **9**:284-302.

————. 1951. Plant distribution in relation to the glacial boundary. Ohio Journ. Sci. **51**:139-146.

————. 1955. The phytogeography of unglaciated eastern United States and its interpretation. Bot. Rev. **21**:297-375.

BRITTAIN, W. H. & W. F. GRANT. 1965a. Observations on Canadian birch (*Betula*) collections at the Morgan Arboretum. I. *B. papyrifera* in eastern Canada. Canad. Field-Naturalist **79**:189-197.

————. 1965b. Observations on Canadian birch (*Betula*) colections at the Morgan Arboretum. II. *B. papyrifera* var. *cordifolia*. Canad. Field-Naturalist **79**:253-257.

————. 1967. Observations on Canadian birch (*Betula*) collections at the Morgan Arboretum. V. *B. papyrifera* and *B. cordifolia* from eastern Canada. Canad. Field-Naturalist **81**: 251-262.

————. 1968. Observations on Canadian birch (*Betula*) collections at the Morgan Arboretum. VII. *B. papyrifera* and *B. resinifera* from northwestern Canada. Canad. Field-Naturalist **82**:185-202.

CAIN, S. A. 1944. Foundations of plant geography. Harper & Bros., N.Y.

CLAUSEN, K. E. 1962a. Introgression in Minnesota birches. Proc. Forest Genetics Workshop, Macon, Ga. pp. 55-58.

————. 1962b. Introgressive hybridization between two Minnesota birches. Silvae Genet. **11**:142-150.

————. 1966. Studies of compatibility in *Betula*. pp. 48-52 *in* Joint Proc. Second Genetics Workshop, Soc. Amer. Foresters and Seventh Lake States Forest Tree Improvement Conference, U. S. Forest Service Research Paper. NC-6. 110 pp.

COOPER, C. F. 1961. The ecology of fire. Sci. Amer. **204**(4):150-160.

DAUBENMIRE, R. F. 1936. The "big woods" of Minnesota: its structure and relation to climate, fire, and soils. Ecol. Monogr. **6**:233-268.

————. 1956. Climate as a determinate of vegetation distribution in eastern Washington and Northern Idaho. Ecol. Monogr. **26**:131-154.

DEEVEY, E. S., JR. 1949. Biogeography of the Pleistocene. Bull. Geol. Soc. Amer. **60**:1315-1416.

DENNY, C. S. 1951. Pleistocene frost action near the border of the Wisconsin drift in Pennsylvania. Ohio Journ. Sci. **51**:116-125.

DETWILER, S. B. 1916. The birches. Amer. Forest. **22**:195-198.

FERNALD, M. L. 1925. Persistence of plants in unglaciated areas of boreal America. Gray Herb. Mem. 2.

GARREN, K. H. 1943. Effects of fire on the vegetation of the southeastern United States. Bot. Rev. **9**:617-654.

GLEASON, H. A. 1922. The vegetative history of the middle west. Ann. Assoc. Amer. Geogr. **12**:39-85.

GOOD, R. 1964. The geography of the flowering plants, 3rd ed. Longman Group Ltd., London. 518 pp.

GOODE, J. P. 1953. Goode's world atlas: physical, political and economic. 9th ed. Rand McNally & Co., New York. 272 pp.

GORHAM, E. 1954. An early view of the relation between plant distribution and environmental factors. Ecology **35**:97-98.

GRABE, D. E. 1961. Tetrazolium and other quick viability tests. Seed World **89**(11):14-15.

HANSON, H. C. 1939. Fire in land use and management. Amer. Midl. Nat. **21**:415-431.

JOHNSON, L. P. V. 1939. A descriptive list of natural and artificial interspecific hybrids in North American forest tree genera. Canad. Journ. Res. C. **17**:411-444.

JOHNSSON, H. 1945. Interspecific hybridization within the genus *Betula*. Hereditas **31**:163-176.

KOEVENIG, J. L. 1975. Distribution of river birch, *Betula nigra*, in the United States. Florida Scientist. **38**:13-19.

KOMAREK, E. V. 1967. Fire and the ecology of man. Proc. 6th Ann. Tall Timbers Fire Ecol. Conf. Tallahassee, Fla. 244 pp.

KREBS, C. J. 1972. Ecology: the experimental analysis of distribution and abundance. Harper & Row, Pub., New York. 694 pp.

LIVINGSTON, B. E. 1916. Physiological temperature indices for the study of plant growth in relation to climatic conditions. Phys. Res. **1**:399-420.

MIROV, N. T. 1967. The genus *Pinus*. Ronald Press, New York. 602 pp.

MULLER, C. R., R. B. HANAWALT & J. K. MCPHERSON. 1968. Allelopathic control of herb growth in the fire cycle of California chaparral. Bull. Torrey Bot. Club **95**:225-231.

OOSTING, H. J. 1958. The study of plant communities: an introduction to plant ecology, 2nd ed. W. H. Freeman and Co., San Francisco. 440 pp.

POLUNIN, N. 1960. Introduction to plant geography and some related sciences. Longmans, Green and Co. Ltd., London. 640 pp.

RAUP, H. M. 1951. Vegetation and cryoplanation. Ohio Journ. Sci. **51**:103-116.

RICHENS, R. H. 1945. Forest tree breeding and genetics. Imp. Agr. Bur., Joint Publ. No. 8. Aberystwyth. 79 pp.

RIGHTER, F. I. 1946. New perspectives in forest tree breeding. Science **104**:1-3.

ROSENDAHL, C. O. 1916. Observation on *Betula* in Minnesota with special reference to some natural hybrids. Minn. Bot. Studies **4**:443-454.

SMITH, E. C. & C. NICHOLS, JR. 1941. Species hybrids in forest trees. Jour. Arnold Arboretum **22**:443-454.

STEBBINS, G. L. 1950. Variation and evolution in plants. Columbia Univ. Press, N. Y. 643 pp.

STEWART, L. 1951. Burning and natural vegetation in the United States. Geogr. Rev. **41**:317-320.

STODDARD, H. L. 1936. Relation of burning to timber and wildlife. Proc. 1st N. A. Wildl. Conf. **1**:1-4.

SWEENEY, J. R. 1956. Responses of vegetation to fire. Univ. Calif. Publ. Bot. **28**:143-250.

SYRACH-LARSEN, C. 1937. The employment of species, types, and individuals in forestry. Roy-Vet. Agr. Coll. Yrbk. Copenhagen. 69-222.

THORNTHWAITE, C. W. 1948. An approach to a rational classification of climate. Geogr. Rev. **38**:55-94.

TIVY, J. 1971. Biogeography: a study of plants in the ecosphere. Oliver & Boyd, Edinburgh. 394 pp.

UNITED STATES DEPARTMENT OF AGRICULTURE, Agricultural Research Service. 1965. Plant Hardiness zone map. U. S. Dept. Agr., Agr. Res. Serv. Misc. Publ. No. 814.

UNITED STATES GEOLOGICAL SURVEY. 1959. United States glacial map, east of the Rocky Mountains. Williams and Heintz, Lithograph Corp., Washington.

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ADDITIONS TO SOME NOTES ON THE FLORA OF THE SOUTHERN STATES, PARTICULARLY ALABAMA AND MIDDLE TENNESSEE[1]

ROBERT KRAL

Some new or otherwise interesting geographic records of vascular plants have been obtained through field work in Alabama and the middle counties of Tennessee, during 1972 and 1973. Additional information comes through other field trips and through records at the Herbarium of Vanderbilt University.

Most of the synonyms listed in this study are from J. K. Small, Manual of the Southeastern Flora (1933); some other synonymy is also provided. Many of the records are the result of checking my own collections against material on deposit at Southern Methodist University. Complete sets of these collections will be on deposit at the Herbarium, Vanderbilt University, with duplicates distributed elsewhere.

Costs of field work on which this paper is based were met in part by a grant to this author by the National Science Foundation (NSF GB-6688x), in part by a grant from the University Research Council, Vanderbilt University, and in part by a stipend from Mr. Raymond Athey of Paducah, Kentucky, an interested and diligent student of the flora of the mid-south. These aids are hereby gratefully acknowledged.

In the preparation of a previous paper (Kral, 1973) I failed to process materials donated to VDB by two excellent field botanists, and therefore did not give proper credit to them for their discoveries of the following species in Alabama: *Amsonia ciliata* Shuttlw. GENEVA CO.: 8 mi s. of Samson, abundant in *Taxodium ascendens-Nyssa biflora-Cyrilla* swamp, 9 May 1967, *S. McDaniel* 8923. *Monarda clinopodia* L. TUSCALOOSA CO.: ravine north of bridge over North River, 9.35 mi. along rte. 82, 11 Jun. 1970, *R. W.*

[1]Received for publication March 20, 1974.

Simmers 1968. *Valerianella pauciflora* Michx. MADISON CO.: bottomland near bridge, e.n.e. New Market in Long Cove Quad, 29 Apr. 1971, *R. W. Simmers* 2296.

These records all predate my own, so that proper credit for discovery in Alabama of these species should have been given. My failure to do this is poor repayment for the kindness of the collectors in sending me specimens.

Marsilea vestita Hook & Grev.

ALABAMA. MOBILE CO.: abundant escape in sandy lots, s. side of old Mobile in negro district ca. 0.5 mi. so. Government Blvd.; forming solid patches along old sidewalks and drives, 2 Jun. 1972, *Kral* 47120.

This pepperwort was stated by Small (1938) to be introduced in central peninsular Florida. It occurs naturally in Texas to British Columbia and Kansas, and in Mexico. The Mobile population appears definitely to be an escape from cultivation and was spreading quite successfully, but urban "renewal" in this same area appears to have wiped it out by 1973. The plants were thriving on quite dry situations, producing an abundance of sporocarps. Dry conditions appear to be necessary for its good growth in the Vanderbilt greenhouse.

Festuca dertonensis (All.) Aschers & Graebn.

ALABAMA. PICKENS CO.: sandy roadbanks, by Ala. 17, 2 mi. n. Aliceville, 28 May 1972, *Kral* 46788.

This fescue, an adventive from Europe, has been found in the northeastern and southwestern United States, with some new stations having been reported from Louisiana, Virginia, and Florida. There is no prior record of it from Alabama.

Eragrostis intermedia Hitchc.

ALABAMA. SUMTER CO.: chalk bluffs, clearing above Tombigbee River, n. of Epes, 5 Oct. 1972, *Kral* 48760.

The Plains Lovegrass is essentially a plant of dry prairies in the southwest. According to Hitchcock (1950), it has been found in Georgia, but there is no prior record of it for Alabama.

Chloris virgata Swartz

ALABAMA. MOBILE CO.: sandy dock loading area by Mobile Bay, south side of Mobile, 10 Oct. 1972, *Kral* 49078.

Hitchcock (1950) reports this essentially western United States weed has been sparingly introduced eastward (Florida to North Carolina in the southeast). This appears to be a first record for Alabama.

Sporobolus neglectus Nash

ALABAMA. DALLAS CO.: chalk hills just n. of old Cahba, s.w. of Selma, 6 Oct. 1972, *Kral* 48826.

Probably an extension southward from Tennessee of this southwestern, midwestern and northern weed.

Gymnopogon chapmanianus Hitchc.

GEORGIA. CHARLTON CO.: sandy, logged slash pineland 5 mi. n. MacClenny on Ga. 185, 13 Sept. 1973, *Kral* 51634.

Seemingly a first record for Georgia of this species known from sandy pinelands in Florida.

Phalaris arundinacea L.

TENNESSEE. OBION CO.: big tufts at edge of sunny slough by Tenn 22 at east side of Union City, 18 Jun. *Kral* 47356.

Indicated as "introduced but not cultivated" for Tennessee by Sharp *et al.* (1960). Not listed for Tennessee by Hitchcock and Chase. This population is fairly large, and appears to be effectively naturalizing.

Panicum helleri Nash

ALABAMA. FRANKLIN CO.: disturbed limestone glade ca. 2 mi. n. Russellville, 17 May 1968, *Kral* 30591. GREENE CO.: chalk prairie by county 19, ca. 4.6 mi. s.e. Boligee, 18 May 1973, *Kral* 50077.

Presumably a first record for this essentially southwestern panic-grass. This and *Panicum scribnerianum* Nash, a more wide-spread species, are extremely close taxonomically, may actually be the same. In any case, neither has been reported for Alabama.

Setaria sphacelata (Schum.) Stapf. & C. E. Hubb.

ALABAMA. MOBILE CO.: sandy dock landing area by Mobile Bay, s. side of Mobile, 10 Oct. 1972, *Kral* 49077.

An African introduction which according to Hitchcock and Chase has escaped cultivation in California (Stanislaus and Kern counties). This appears to be a first record for it in the southeastern United States. It appears to be spreading onto sandy lots in the city of Mobile, in that I have seen it in additional localities there in 1973. A description of a very similar plant is given by Mohr (1901) under the name *Chaetochloa gracilis* (H.B.K.) Scribn. & Merrill, based on collections by Mohr in Mobile. This last is in the synonymy of *Setaria geniculata* (Lam.) Beauv., which might be an indication of a nomenclatural problem yet to be resolved. My own specimens agree with Californian material of *S. sphacelata* deposited at the Herbarium, SMU.

Andropogon mohrii (Hack.) Hack. ex Vasey

FLORIDA. FRANKLIN CO.: sandy peat of pineland savanna by Fla. 65, 18.6 mi. s. Sumatra, 13 Oct. 1973, *Kral* 52387.

This constitutes a first report for this grass for Florida; presumably it is an extension southward from the pine barrens of Alabama or Georgia.

Heteropogon contortus (L.) Beauv. ex R. & S.

FLORIDA. MARTIN CO.: sandy slash pine lot and roadbank near Stuart Police Dept. grounds, Stuart, 21 Jan. 1972, *Kral* 45071.

This perennial weed has been reported by Hitchcock from the southwestern United States. It is a frequent weed in Latin America and in the old world tropics. This is a first record of it for the southeastern United States.

Dichromena colorata (L.) Hitchc.

ALABAMA. SHELBY CO.: ca. 1 mi. s. Harpersville by Ala. 25; wet open swale by creek, 11 Aug. 1973, *Kral* 51160.

ST. CLAIR CO.: ca. 5 mi. n.e. Leeds by US 411; low cleared area over limestone, 13 Jul. 1972, *Kral* 47686.

Already reported for an inland station in Alabama (Kral, 1973) but these stations are so much farther inland in the Appalachians as to merit mention here. Mohr long ago indicated its occurrence as far inland as Scottsboro.

Carex aestivalis M. A. Curtis

ALABAMA. JACKSON CO.: sandy woods, s.w. facing slope of mountain by Ala. 146, s. of Estill Fork, 14 Apr. 1973, *Kral* 49566.

An extension southward from Tennessee.

Carex eburna Boott

ALABAMA. BIBB CO.: shelves of steep limestone bluff on Cahaba River near Pratts Ferry, *R. M. Harper* 3552; on limestone bluff over Cahaba River at site of former Pratts Ferry, near route 27 bridge, 17 Apr. 1973, *J. A. Churchill* 73-4170.

This slender, caespitose *Carex* has been thought previously to extend southward only to Virginia, Tennessee, Missouri and Nebraska. The Pratts Ferry locality represents a sizeable extension southward.

Carex gracilescens Steud.

C. laxiflora Lam. var. *gracillima* (Boott) Robins. & Fern.

ALABAMA. MARSHALL CO.: Bucks Pocket State Park; sandrock slopes of ravine along trail to boat landing & picnic area by reservoir, 15 Apr. 1973, *Kral* 49630.

Dr. McDaniel has informed me of still further (and older) records for this species in Alabama: GREENE CO.: wooded ravine just north of Knoxville, 20 Mr. 1938, *Harper* 3620 (US); LAUDERDALE CO.: near top of rocky bluff facing north, on Indian Camp Creek, ca. 4 mi. south of Pruitton, 13 Apr. 1935, *Harper* 3327 (US); MADISON CO.: calcareous rather open woods on west slope of Pantherknob, on eastern spur of Monte Sano, 24 Apr. 1940, *Harper* 3782 (MO, US).

Carex microdonta Torr. & Hook.

ALABAMA. CLARK CO.: calcareous glade by US 84, 3.6 mi. w. Gosport, 31 May 1972, *Kral* 47027. HALE CO.: prairie remnant by Ala. 69, 1.8 mi. s. Greensboro, 29 May 1972, *Kral* 46845.

Further county records for this sedge of the western grasslands reported as new for Alabama in my previous article (1973).

Carex pedunculata Muhl.

ALABAMA. JACKSON CO.: north facing, essentially calcareous bluff above Estill Creek, north of Estill Fork near where gravel road fords creek, 14 Apr. 1973, *Kral* 49546.

This distinctive carex, hitherto not reported for Alabama, represents a considerable range extension southward for a species said by Gleason (1952) to be of rich woods and calcareous soil, Newfoundland to Minnesota and South Dakota, s. to Virginia, West Virginia and Iowa and to be "abundant in the Great Lakes Region".

Carex prasina Wahl.

ALABAMA. COLBERT CO.: shaded creekbanks, in shallow water on Bear Creek Ranch, s.w. side Littleville, 27 May 1972, *Kral* 46736.

A distinctive member of the sect. *Gracillimae*, hitherto not reported for Alabama, and probably an extension southward from middle Tennessee where it is not rare along streams of cool, steep-sided ravines.

Carex purpurifera Mackenzie

C. laxiflora Lam. var. *purpurifera* (Mackenzie) Gl.

ALABAMA. JACKSON CO.: richly wooded bluff, 9 mi. s. Huntland by Ala. 65, 28 Apr. 1972, *Kral* 45790. MADISON CO.: north facing slope south of Rocky Branch, King Cove Quadrangle area, 9 Apr. 1971, *R. W. Simmers* 2209; 29 Apr. 1971, *R. W. Simmers* 2278.

An extension southward from Tennessee for this carex, which is perhaps doubtfully distinguished from *C. graci-*

lescens Steud. The latter has shorter perigyna and narrower pistillate bracts, but otherwise seems much the same. Dr. McDaniel informs me that he has seen earlier records for Alabama, namely MARSHALL CO.: among limestone rocks in rich woods around sink in Fletchers Hollow, west of Grant, 19 Apr. 1935, *Harper* 3345 (US).

Lachnocaulon anceps (Walt.) Morong

TENNESSEE. CUMBERLAND CO.: open, sphagnous, boggy bottom by Interstate 40, 3 mi. e. jct. US 127, the Crossville exit, 2 Aug. 1973, *R.* & *G. Kral* 50961.

An extension northward from Alabama for this essentially coastal plain genus. This species, together with *Eriocaulon decangulare* L. is occasional in acid seeps in northeastern Alabama.

Juncus brachycephalus (Engelm.) Buch.

GEORGIA. GORDON CO.: 14 mi. s. Chatsworth by US 411; sunny seep, 8 Sept. 1973, *Kral* 51520.

A first report for Georgia for this rush which, according to Gleason (vol. 1, p. 396, 1952) is found "in wet meadows and sandy shores, Me. to n. Ont. and Minn., s. to Pa., O., and Ind." It was recently reported for Tennessee by Kral (1973).

Pleea tenuifolia Michx.

ALABAMA. BALDWIN CO.: longleaf pineland bog ca. 2 mi. w. of Seminole, 9 Oct. 1972, *Kral* 49003.

A first published report for this species for Alabama, and probably an extension from nearby Florida. First found in this locality by Dr. S. McDaniel (3 mi. west of Seminole, common in *Sarracenia* bog, *McDaniel* 3916).

Lilium regale Wils.

ALABAMA. LAMAR CO.: by Ala. 17, in gravelly roadside and scattered through adjacent oak-pineland, 3.9 mi. s. Hamilton, 16 Aug. 1973, *Kral* 51377.

An evident escape from cultivation, but so successfully spreading as to deserve mention here. The narrowly fun-

nelform, large perianths are horizontal to somewhat nodding on the pedicels and toward dusk (which was when I collected vouchers) emit an extremely heavy, sweet fragrance.

Arabis hirsuta (L.) Scop.

TENNESSEE. RUTHERFORD CO.: cut-over cedar woods and adjacent limestone glades by Interstate 24, 13 mi. n.w. jct. US 231, the Murphreesboro exit, 27 Apr. 1973, *Kral* 49729.

A first record for Tennessee for this rock-cress. In character of trichomes (which are sparse) it appears closest to the var. *adpressipilis* (Hopkins) Rollins. The population is a large one and doubtless more will be found in the limestone barrens of middle Tennessee.

Erysimum capitatum (Dougl.) Greene

E. arkansanum Nutt.

TENNESSEE. PUTNAM CO.: limestone bluffs above the Caney Fork River by Interstate 40, 9 mi. e. jct. Tenn. 53 (the Gordonsville-Carthage exit), 27 Apr. 1973, *Kral* 49699.

A first record for Tennessee, and a fairly wide disjunction either eastward from Missouri or southward from southern Illinois. A very handsome plant, the flowers deliciously fragrant, the petals a deep orange-red.

Potentilla intermedia L.

TENNESSEE. DAVIDSON CO.: cindery sands of railroad yards, downtown Nashville, 30 Aug. 1973, *Kral* 51491.

An introduced weed from Europe with scattered localities from Quebec southward to Michigan and Virginia. A first record for Tennessee.

Trifolium vesciculosum Sari

ALABAMA. PIKE CO.: highway shoulder of US 231, n.w. side of Troy above Conecuh River bottoms, 6 Jun. 1972, *Kral* 47355. BUTLER CO.: north side Greenville; sandy highway shoulders, 19 May 1973, *Kral* 50171. SHELBY CO.:

just e. of Bibb Co. line, e. of Green Pond and Turner; sandy road shoulders, 21 May 1973, *Kral* 50295. WILCOX CO.: by Ala. 10, road embankment ca. 2 mi. e. Ala. 5, and w. of Camden, 8 Jun. 1973, *Kral* 50442.

Already reported by Kral (1973) for Alabama, but these localities are added to indicate the success of this species as a new weed of roadsides in the state.

Dalea alopecuroides Willd.

TENNESSEE. HUMPHRIES CO.: sandy roadbank and adjacent fields, Tennessee Ridge road, south end, ca. 9 mi. n. of Waverly, 6 Sept. 1972, *Kral* 48361.

Mahler (1970) excludes this species from the Tennessee Flora, indicating that the Gattinger (1901) report of its abundance in western Tennessee was possibly in error. While this writer has seen but one population, it was a large one extending for at least two miles along the road and in adjacent fields, and therefore there is some indication that the species might naturalize successfully on a local scale.

Anoda cristata (L.) Schlecht.

TENNESSEE. STEWART CO.: just s.e. Dover on silty sandy backwater shores of Lake Brakley, 4 Oct. 1973, *Kral* 52242.

An extension of known range southward from Kentucky. According to Gleason (1952) this weed of the southwestern states, Central America and South America is reported as a waif around woolen mills in the east, also in Missouri and Iowa. This is a first record for Tennessee.

Hibiscus coccineus Walt.

ALABAMA. COVINGTON CO.: sandy banks and shallows of Open Pond, Blue Springs Game Mgmt. area, Conecuh National Forest, s.w. Andalusia, 17 Jul. 1970, *Kral* 40079.

This bright-red flowered *Hibiscus*, frequently cultivated, has been known in the wild in the United States only from peninsular Florida, according to Duane Wise, monographer of the genus. The plants of the Alabama locality were

growing mostly in the shoals of a natural, limesink pond, this at a considerable distance from any evident habitation.

Ludwigia polycarpa Short & Peter

Isnardia polycarpa Kuntze

ALABAMA. COVINGTON CO.: very abundant, but one stand only, in peaty ditch, pine flatwoods, beside county 42, 15 mi. e. Brooklyn, 1 Sept. 1970, *Kral* 40992.

A first report for Alabama of this species, hitherto known from Massachusetts and Connecticut, Ontario to Tennessee and Kansas.

Oenothera grandiflora Ait.

TENNESSEE. MARION CO.: by Interstate 24E, just 1 mi. s.s.e. Monteagle; rocky bluffs above highway, 10 Jul. 1972, *Kral* 47557.

This population, spectacular when in bloom because of the large pale yellow corollas, is a first definite record for Tennessee of a species known in the wild only from the Mobile delta country of Alabama. The Tennessee specimens fit the type description perfectly having sepal lobes well over 3 cm long, filiform-tipped, and the corollas when pressed fully 9-10 cm broad.

Oenothera heterophylla Spach

Rehmannia heterophylla (Spach) Rose

ALABAMA. GREENE CO.: sandy railroad right of way, bottoms of Tombigbee River, just n. of US 11 crossing north of Epes and s. of Bolegee, 18 May 1973, *Kral* 50093. PICKENS CO.: sandy borrow pit by Ala. 17, ca. 4 mi. s. Aliceville, 3 May 1972, *Kral* 46243. SUMTER CO.: sandy clay field 5.2 mi. s. Dancy, 3 May 1972, *Kral* 46386.

The large size of the petals of the Alabama plants together with the comparatively long sepal tips, definitely distinguish them from *Oe. rhombipetala* which has been reported adventive to the east, and which is perhaps to be looked for in Alabama. According to Munz (1965) this species has been known, prior to the Alabama finds, only from eastern Texas and Calcasieu Parish, Louisiana.

Cornus purpusi Koehne

TENNESSEE. HUMPHRIES CO.: shrub of gravelly bottoms of Richland Creek ca. 7 mi. n.e. Waverly, 6 Sept. 1972, *Kral* 48363.

Another middle Tennessee record for this shrub reported as new for Tennessee by Kral (1973).

Perideridia americana (Nutt.) Reichenb.

Eulophus americanus Nutt. ex DC.

ALABAMA. COLBERT CO.: mesic woods by small limestone outcrop by Natchez Trace Parkway, ca. 5.5 mi. s.w. Colbert Park, 26 May, 1972, *Kral* 46666.

A species that appears to frequent limestone outcrop areas, mostly in the plains states and Ozarks, very rare in middle Tennessee, and now reported from this northwestern county of Alabama.

Lysimachia quadriflora Sims

Steironema quadriflorum (Sims) Hitchc.

ALABAMA. JEFFERSON CO.: south side of Leeds; wet limestone barren by Ala. 119, 13 Jul. 1972, *Kral* 47671. ST. CLAIR CO.: ca. 5 mi. n.e. Leeds by US 411; low grounds, 13 Jul. 1972, *Kral* 47686.

Additional county information on this species, recently reported as new for Alabama (Kral, 1973).

Eustoma exaltatum (L.) Griseb.

ALABAMA. MOBILE CO.: south side Mobile, in docks area on moist sands just n. of n. boundary of old Air Force Base, 15 Aug. 1973, *Kral* 51346.

A first record for Alabama of this striking annual which hitherto has been known in the United States only from the coasts of Florida and Texas. This population consisted of many hundreds of individuals. It has also been collected from Louisiana and Mississippi in recent years.

Sabatia grandiflora (A. Gray) Small

ALABAMA. HOUSTON CO.: edge of limesink pond by county 4, ca. 5 mi. w.n.w. Chattahoochee State Park entrance, 8 Oct. 1972, *Kral* 48950.

Dr. Wilbur (1955) reports this species for peninsular Florida and western Cuba. However, since his revision was published, the species has been found to be quite frequent in the Florida panhandle, and the above collection now adds Alabama to its range.

Ipomoea cairica (L.) Sweet

ALABAMA. MOBILE CO.: sandy area by boat docks along bay, edge of negro sector and s. of Government Street, 2 Jun. 1972, *Kral* 47114.

This native of Africa is reported in Small as only from Florida for the United States. The corolla limb is a pale lavender, this grading into an almost white throat and tube.

Blephilia hirsuta (Pursh) Benth.

ALABAMA. JACKSON CO.: abundant on sunny moist bluffs above creek, ca. 9.2 mi. s. Huntland, 11 Jul. 1972, *Kral* 47574.

While *Blephilia ciliata* ranges widely through the southeast, this species appears to be confined to the mountain districts in the south. I know of no other records for it in Alabama.

Stachys agraria Cham. & Schlecht.

ALABAMA. MONTGOMERY CO.: sandy low rise in low pasture by Loop bypass, s. side Montgomery, 1 May 1972, *Kral* 46142.

Small (1933) reports this as introduced into the coastal plain of Alabama, with a main range extending from Louisiana into Texas. This locality adds to the limited information about the species in Alabama.

Synandra hispidula (Michx.) Britt.

Synandra grandiflora Nutt.

ALABAMA. JACKSON CO.: locally abundant in rocky wet ravine above Ala. 65, 9 mi. s. Huntland, 28 Apr. 1972, *Kral* 45795.

This showy mint, hitherto not reported for Alabama, is stated in Small (1933) as being in the Interior Low Plateau and adjacent provinces, Tennessee to Illinois, Ohio and Virginia.

Agalinis heterophylla Small

Gerardia heterophylla Nutt.

ALABAMA. MARENGO CO.: chalk glades, w. side Demopclis by US 80, 6 Oct. 1972, *Kral* 48870. GREEN CO.: prairie remnant, 7.4 mi. n.n.e. Prairieville by Ala 69, 20 Sept. 1971, *Kral* 44454. HALE CO.: chalk prairie by US 80, 0.5 mi. w. Prairieville, 6 Oct. 1972, *Kral* 48858; prairie remnant by county 61, ca. 8.5 mi. n. Uniontown, 6 Oct. 1972, *Kral* 48854. SUMTER CO.: chalk prairie, by Ala. 17, 8.7 mi. s. Dancy, 5 Oct. 1972, *Kral* 48777.

The Prairie Agalinis, according to Correll & Johnston (1970) is supposed to range from Missouri and Oklahoma to Louisiana and Texas. My records, therefore, constitute a first report for Alabama, an easternmost disjunction. Superficially it resembles *Agalinis purpurea*, but is coarser, stiffer, with broader leaves and quite elongate calyx lobes.

Penstemon multiflorus Chapm.

ALABAMA. BALDWIN CO.: sandy longleaf pineland, clearing by highway, Seminole, 10 Jun. 1973, *Kral* 50478. COVINGTON CO.: sandy bank by county 4, ca. 8 mi. w. Florala, 8 Jun. 1969, *Kral* 35164.

This species is easily distinguished by its pouch-like anthers which dehisce by short proximal slits, and by its relatively long inflorescence branches. According to Small (1933) its range is confined to Florida and south Georgia.

Galium parisiense L.

ALABAMA. SUMTER CO.: north side of Epes by US 11 crossing of Tombigbee River; exposed chalk bluff area, 18 May 1973, *Kral* 50109.

To my knowledge a first record for Alabama of this European weed, which is locally abundant in the limestone glades of middle Tennessee.

Galium virgatum Nutt.

ALABAMA. FRANKLIN CO.: limestone glades at Isbell, 27 May 1972, *Kral* 46768. SUMTER CO.: 7 mi. n. Livingston; chalk prairie by US 11, 18 May 1973, *Kral* 50115.

This bedstraw of calcareous Ozarkian areas, locally abundant in the limestone barrens of middle Tennessee, has not been reported previously for Alabama.

Dyschoriste oblongifolia (Michx.) O. Kuntze

Ruellia oblongifolia Michx.

ALABAMA. HENRY CO.: longleaf pine sandhills 3.6 mi. n.n.e. Abbeville beside county 46, 2 May 1972, *R. Kral* 46213. HOUSTON CO.: sandy edge of field in longleaf pineland ca. 1 mi. w. Columbia by Ala. 52, 2 May 1972, *R. Kral* 46182.

This species, frequent in sandy longleaf pinelands from Florida north to coastal plain South Carolina (possibly in southeastern Virginia), has been reported for Alabama by Kobuski (1928) on the basis of a Buckley record which lacks date and locality. A specimen of it collected by Mohr from the Mobile area is in the Mohr herbarium, but is identified as a *Ruellia* and was not cited by him in his Flora. In that it is not recorded for the state of Alabama in current manual treatments, these collections give it genuine status for the Alabama flora.

Ruellia brittoniana Leonard

GEORGIA. GRADY CO.: banks of ditch, north side of Cairo, 8 Aug. 1972, *Kral* 47962.

This handsome species, erroneously treated by Small (1933) as *Ruellia malacosperma* Greenm., hitherto has been known only from the lower coastal plain from Florida into Texas.

Lobelia glandulosa Walt.

ALABAMA. HOUSTON CO.: edge of limesink pond by county 4, ca. 5 mi. w.n.w. Chattahoochee State Park entrance, 8 Oct. 1972, *Kral* 48948.

This species, not previously reported for Alabama, is cited by McVaugh (1936) from wetlands in pines, Florida to southern Virginia, with doubtful records from Mississippi and Texas.

Valerianella dentata (L.) Poll

TENNESSEE. TROUSDALE CO.: north banks of Cumberland River by Tenn. 141 0.5 mi. s. Hartsville; pastured limestone bluff area, common, 4 May 1973, *Kral* 49797.

This species has been reported previously from Alabama (GREENE CO.: Eutaw, *R. Harper* 3148. CLARKE CO.: W. Duncan) and Tennessee (DAVIDSON CO.: Una J. Cibulka 130) by Dr. Donna Ware (1969), but was excluded by her in her treatment of *Valerianella* in North America because of uncertain establishment of this waif. However, the Trousdale locality has the species in abundance and it should be looked for in similar localities in Alabama and Tennessee. *Valerianella dentata* differs from other valerianellas of the area in its narrower leaves, in its irregular, ovate, toothlike prolongation of the calyx, and in its strigillose carpel bodies, the hairs of which are incurved. The corollas have tube and throat narrowly funnelform, and range from pale lavender to pink.

Elephantopus spicatus Juss. ex Aubl.

Pseudolephantopus spicatus (Juss.) Rohr

FLORIDA. MARTIN CO.: weed of Owen's Grove, Indiantown; sandy ground in orange grove and in hammock edges, 22 Jan. 1972, *Kral* 45089; 19 Jan. 1973, *Kral* 49264.

Dr. Sidney McDaniel and Dr. Jerry Clonts of Mississippi State University have kindly informed me that this is not a first report for the United States, the species having been collected in and reported for south Florida by Dr. S. F. Blake (1948). It is, however, not reported by Drs. Long and Lakela in their current *Flora of Tropical Florida* (1971); this new locality for it is cited merely to verify the continued presence of the species in Florida.

Eupatorium leptophyllum DC.

ALABAMA. COVINGTON CO.: Blue Pond, Blue Springs Game Mgmt. area, Conecuh Nat. Forest s.w. Andalusia, 3 Oct. 1971, *Kral* 44742; HOUSTON CO.: edge of limesink pond by county 4, ca. 5 mi. w.n.w. Chattahoochee State Park entrance, 8 Oct. 1972, *Kral* 48952.

Dr. R. K. Godfrey, current monographer of *Eupatorium* for North America has indicated to me that, whilst Small (1933) indicated the range of *E. leptophyllum* as extending from Florida to Mississippi and South Carolina, he had no record of its occurrence in Alabama. Mohr cited it as being of rather general distribution in lower coastal plain Alabama, but this might involve some error in identification since the species appears more confined to the limited rash of limestone "solution" ponds in south Alabama.

Liatris cylindracea Michx.

ALABAMA. BIBB CO.: ca. 5 mi. n. Centerville by jct. Ala. 219 and Ala. 5; calcareous rocky clearing in longleaf pineland, 8 Oct. 1973, *Kral* 52262.

Gaiser (1946) reports this species as occurring from southern Ontario and western New York westward to Minnesota and Missouri, so this find is a significant disjunction. The species is unmistakable, combining a plumose pappus with a cymose-racemose inflorescence and closely appressed rounded phyllaries.

Heterotheca latifolia Buckley

TENNESSEE. DAVIDSON CO.: cindery sands of railroad yards, downtown Nashville, 30 Aug. 1973, *Kral* 51501. SHELBY CO.: stabilized sandy areas on Presidents Island, P.O. Memphis, 25 Oct. 1952, *Demaree* 33188.

The range of this camphor-weed appears to be rapidly expanding in the mid-south. In the southeastern and Gulf coastal plain it is becoming one of the most abundant weeds of sandy old fields and along roadsides. The two above-cited collections verify its presence as a weed in middle and western Tennessee.

Heterotheca pilosa (Nutt.) Shinners

Chrysopsis pilosa Nutt. (not *C. pilosa* (Walt.) Britt.)

TENNESSEE. LAWRENCE CO.: sandy clay field ca. 5 mi. s.s.w. Summertown, 14 Sept. 1972. *Kral* 48412.

A first report for Tennessee for this tall, annual camphor-weed. Sharp et al. (1960) report *Chrysopsis pilosa* (Walt.) Britton from several counties in Tennessee, but this report is based on a species whose actual name is *Heterotheca camporum* (Greene) Shinners, our commonest weedy perennial camphor-weed. The actual *H. pilosa* is most abundant west of the Mississippi River in sandy open places from Missouri south to Louisiana and Texas.

Ambrosia bidentata Michx.

TENNESSEE. LAWRENCE CO.: gravelly pasture off US 43, just s. of Summertown, 27 Jul. 1972, *Kral* 47819.

An additional record for this species in Tennessee (see Kral, 1973, p. 407). Its spread in the state appears assured.

Rudbeckia mollis Ell.

ALABAMA. HOUSTON CO.: north side of Dothan; sandy edge of oak-pine hammock, 12 Aug. 1973, *Kral* 51183.

An additional county record in Alabama for this *Rudbeckia* which before was known only from Florida and Georgia (see Kral, 1973, p. 407).

Dyssodia aurea (Gray) A. Nels.

Hymenatherum aureum (Gray) Gray

ALABAMA. MOBILE CO.: dry sandy area of Mobile docks, just north of north boundary of old Air Force Base, 15 Aug. 1973, *Kral* 51347.

In regard to pappus character my specimens are intermediate between the var. *aurea* and var. *polychaeta* (Gray) M. C. Johnston as they are described by Dr. Strother (1969). This is a first report for Alabama for this plant of the high plains of the western United States and northern Mexico. The Mobile population covers at least an acre, the locality being shared by *Helenium amarum* and *Eustoma exaltata.*

Lactuca saligna L.

ALABAMA. LIMESTONE CO.: calcareous banks of Interstate 65, 0.5 mi. n. Holland Gin, 26 Sept. 1972, *Kral* 48563. MORGAN CO.: gravelly highway shoulder by backwater bottom of Flint Creek, Lacon, 8 Oct. 1973. *Kral* 52280.

A first report for Alabama, the species is probably moving southward from Tennessee in the limestone districts where it abounds. A native of Europe.

LITERATURE CITED

BLAKE, S. F. 1948. *Pseudo-elephantopus spicatus*, a weed of potential importance in Florida. Rhodora **50**: 280-282.

CORRELL, D. S. & M. C. JOHNSTON. 1970. Manual of the vascular plants of Texas. Geo. Banta Company, Menasha, Wisc.

GAISER, L. O. 1946. The genus *Liatris*. Rhodora **48**: 165-183; 216-263; 273-326; 331-382; 393-412.

GATTINGER, A. 1901. The flora of Tennessee. Nashville.

GLEASON, H. A. 1952. Illustrated Flora of the northeastern United States and adjacent Canada, Vol. 1. Lancaster Press.

HITCHCOCK, A. S. 1950. Manual of the grasses of the United States, ed. 2 (Revised by Agnes Chase). U.S. Dep. Agr. Misc. Publ. 200.

KOBUSKI, C. E. 1928. A monograph of the American species of the genus *Dyschoriste*. Ann. Mo. Bot. Gard. **15**: 9-90.

KRAL, R. 1973. Some notes on the flora of the southern states, particularly Alabama and middle Tennessee. Rhodora **75**: 366-410.

LONG, R. W. & O. LAKELA. 1971. A flora of tropical Florida. University of Miami Press.

MAHLER, W. F. 1970. Manual of the legumes of Tennessee. Journ. Tenn. Acad. Sci. XLV (3): 65-96.

MOHR, C. 1901. Plant life of Alabama. Contr. U.S. Natl. Herb. **6**: 1-921.

MUNZ, P. A. 1965. Onagraceae in North American Flora. Ser. II (5): 1-231. New York Botanical Garden.

SHARP, A. J., R. E. SHANKS, J. K. UNDERWOOD, & E. MCGILLIARD. 1960. A preliminary checklist of monocots and dicots in Tennessee. Mimeograph.

SMALL, J. K. 1933. Manual of the southeastern flora. Chapel Hill.

————. 1938. Ferns of the southeastern states. Science Press. Lancaster, Pa.

STROTHER, J. L. 1969. Systematics of *Dyssodia* Cavanilles (Compositae: Tageteae). Univ. Calif. Publ. in Botany **48**: 1-88.

Ware, D. M. E. 1969. A revision of the genus *Valerianella* (Valerianaceae) for North America. Unpublished Ph.D. thesis, Vanderbilt University. 249 pp.

Wilbur, R. L. 1955. A revision of the north American genus *Sabatia* (Gentianaceae). Rhodora **57**: 1-103.

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STUDIES IN THE RANUNCULACEAE OF THE SOUTHEASTERN UNITED STATES II. THALICTRUM L.[1,2]

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While completing a treatment of the Ranunculaceae for the forthcoming *Vascular Flora of the Southeastern United States,* certain nomenclatural and taxonomic decisions had to be made which call for additional clarification. This treatment of *Thalictrum* is conservative in that I follow a species concept allowing for considerable intraspecific population variability. Unless populations show discrete geographic patterns correlated with morphological discontinuities, I see no compelling reason to describe subspecies, varieties, etc. Furthermore, unless breeding studies suggest intraspecific relationships, I prefer to recognize morphologically defined species. The aim throughout is to provide a rationale for certain taxonomic and nomenclatural conclusions, plus a key to the species and their distribution within the southeastern United States.

As a genus, *Thalictrum* can be distinguished from other Ranunculaceae by its alternate, ternately compound or decompound leaves, actinomorphic apetalous bisexual or unisexual flowers with numerous well-developed stamen filaments and non-plumose achenes crowded on small receptacles. Although 120 species of *Thalictrum* have been described for the world (Buchheim, 1964), I am recognizing only 14 species within the southeastern United States, an area bounded by and including Louisiana, Arkansas, Kentucky, West Virginia, Maryland, and Delaware.

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[1]Based on a manuscript and notes compiled for the forthcoming *Vascular Flora of the Southeastern United States.* In general, the format follows Radford et al. (1967). Any suggestions relating to this treatment should be sent to me so that necessary corrections and additions can be made before the *Vascular Flora* is in press.

[2]Contribution No. 117 from the Department of Biology, The Pennsylvania State University.

Table I.

Chromosome Numbers of the Species of *Thalictrum* in the Southeastern United States

Species	Chromosome Number	Reference
T. *arkansanum*	—	
T. clavatum	$n = 7$	Jensen (1944)
T. cooleyi	—	
T. coriaceum	$2n = 70$	Gregory (1941)
	$n = 70$	Jensen (1944)
T. dasycarpum	$2n =$ ca. 100	Zhukova (1961), cited in Cave (1962)
		Zhukova (1967), cited in Ornduff (1969)
T. debile	—	
T. dioicum	$n = 14$	Jensen (1944)
	$2n = 42$	Kuhn (1928), cited in Gregory (1941)
	$2n = 42$	Zhukova (1967), cited in Ornduff (1969)
T. macrostylum	—	
T. mirabile	—	
T. pubescens (= *T. polygamum*)	$n = 42$	Jensen (1942)
	$2n = 84$	Löve & Löve (1966), cited in Ornduff (1968)
	$2n = 154$	Gregory (1941)
T. revolutum	$2n =$ ca. 133	Gregory (1941)
T. subrotundum	—	
T. steeleanum	—	
T. thalictroides (= *T. anemonoides, Anemonella thalictroides*)	$2n = 14$	Gregory (1941)
	$2n = 14$	Sorokin (1929)
	$2n = 42$	Kuhn (1928), cited in Gregory (1944)

Even though *Thalictrum* has been treated by Lecoyer (1885), Trelease (1886), Gray (1895), Davis (1900), and most recently by Boivin (1944), the species in eastern North America still need a thorough study from a modern biosystematics standpoint. This is especially the case for the *T. debile* complex, *T. pubescens, T. dasycarpum, T. coriaceum,* and the *T. macrostylum* complex. Although Kaplan and Mulcahy (1971) studied pollination and floral sexuality in selected species, I know of no recent population-based biosystematic studies of any species of *Thalictrum* in eastern North America. Furthermore, chromosome counts for seven species are needed, and several other species (*T. revolutum, T. pubescens, T. dasycarpum*) should be reassessed (Table I).

KEY TO SPECIES

1. Inflorescence umbelliform; plants usually less than 2(-3) dm tall. .... 1. *T. thalictroides.*
1. Inflorescence paniculate; plants usually more than 2 dm tall.
    2. Flowers perfect; sepals 5; fruits long-stipitate, flat, with a minute stigma.
        3. Dorsal margin of mature fruits concave, up to twice the stipe in length; filaments usually more than 3 mm long. .... 2. *T. clavatum.*
        3. Dorsal margin of mature fruits straight, about equalling the stipe in length; filaments usually less than 3 mm long. .... 3. *T. mirabile.*
    2. Flowers imperfect, rarely perfect; sepals 4(-6); fruits sessile or short-stipitate, plump, tipped by a long stigmatose style.
        4. Leaflets 3 (or more)-lobed apically, the lobes often crenate; filaments colored, filiform; plants dioecious, rarely polygamous.

5. Achenes sessile; upper cauline leaves often long-petioled; plants flowering in early spring.
   6. Plants erect, usually over 3 dm tall; roots fibrous; largest leaflets over 15 mm wide. .... 4. *T. dioicum.*
   6. Plants lax, usually less than 3 dm tall; roots tuberous; largest leaflets less than 15 mm wide.
      7. Mature fruits elliptic-lanceolate, 0.7-1.2 mm broad; sepals usually 1-2 mm long. .... 5. *T. debile.*
      7. Mature fruits ellipsoid, 1.5-2 mm broad; sepals usually 1-3 mm long. .. .. 6. *T. arkansanum.*
5. Achenes stipitate, the stipes wing-angled; upper cauline leaves sessile or subsessile; plants normally flowering in early summer.
   8. Plants caudiciferous, but not rhizomatous; terminal leaflets mostly longer than wide; anthers 2-3.5 mm long. .. 7. *T. coriaceum.*
   8. Plants rhizomatous; terminal leaflets mostly shorter than wide; anthers 3.2-5 mm long. .... 8. *T. steeleanum.*

4. Leaflets entire or 3-lobed apically, the lobes entire (rarely crenate); filaments usually white, often more or less clavate; plants usually polygamous or polygamodioecious.
   9. Leaflets usually stipitate-glandular beneath (or occasionally muricate or whitened papillose, rarely pubescent otherwise), coriaceous with strongly revolute margins; achenes more or less sessile, often stipitate-glandular; anthers 1.8-2.8 mm long. .. 9. *T. revolutum.*
   9. Leaflets glabrous or pubescent beneath, their texture and margins various; achenes short-stipitate to sessile, glabrous to pubescent; anthers either 0.5-1.5 or 1.5-3.5 mm long.

10. Leaflets narrowly lanceolate to oblanceolate, 5-10 times longer than wide. .... 10. *T. cooleyi.*

10. Leaflets suborbicular to obovate, usually less than 2 times longer than wide.

11. Leaflets usually entire or occasionally 3-lobed apically, glabrous beneath, the largest usually less than 15 mm wide; sepals 1-2 mm long.

12. Plants rigid, erect; leaves usually coriaceous, greyish to brownish or yellowish green, usually prominently reticulate beneath; filaments rigid, usually distinctly clavate. .... 11. *T. macrostylum.*

12. Plants lax, reclining; leaves usually thin, membranous, greenish, not prominently reticulate beneath; filaments flexuous, scarcely clavate. .... 12. *T. subrotundum.*

11. Leaflets 3-lobed apically, usually pubescent beneath, the largest 15-40 mm or more wide; sepals 2-5 mm long.

13. Stigmas about ½ length of the achene body; filaments rigid, ascending, strongly clavate; anthers usually less than 1.5 mm long. ... 13. *T. pubescens.*

13. Stigmas nearly as long as the achene body; filaments flexuous, filiform, scarcely dilated distally; anthers 1.5-3.5 mm long. .... 14. *T. dasycarpum.*

1. **T. thalictroides** (L.) Eames and Boivin, Rue Anemone.

Woods, banks, and thickets; chiefly mts. and pied. Ark., Fla., Ga. pied., Ky. pied., Md., N. C., S. C., Tenn., Va., W. Va. [All except Tex.] *Anemonella thalictroides* (L.) Spach — Fernald (1950), Gleason and Cronquist (1963); *Syndesmon thalictroides* (L.) Hoffmgg. — Small (1933).

No other species of the Ranunculaceae in our flora has been placed among as many genera as the common Rue Anemone. Linnaeus (Sp. Pl. **1**: 542. 1753) initially described it an an *Anemone,* but on cytological and morphological grounds its affinities are clearly elsewhere (Gregory, 1941; Boivin, 1957*b;* Tamura, 1968). Michaux (Fl. Bor.-Am. **1**: 322. 1803) treated the species as a member of *Thalictrum* (as *T. anemonoides*), and later Hoffmannsegg (Flora **15**: Pt. 2, Intell. n. 4, p. 34. 1832) placed it in his new genus *Syndesmon,* a *nomen nudum* taken up later by Britton (1891) and others. Eventually Spach (Hist. Nat. Vég. **2**: 339. 1839) erected the genus *Anemonella* which was accepted by Gray (1886) and subsequently adopted in various regional manuals (*e.g.,* Fernald, 1950; Gleason and Cronquist, 1963).

The taxonomic question therefore is whether the Rue Anemone is sufficiently distinctive to warrant its separation from *Thalictrum* as Gray (1886) and others maintained. Boivin (1957*b*) reviewed this problem and concluded on the basis of its tuberous roots, compound leaves, sepal, stamen, carpel and fruit characteristics, the Rue Anemone should be classified in *Thalictrum* section *Physocarpum* DC. Moreover, as Eames (quoted in Boivin, 1957*b*) pointed out, the involucral leaves are not truly opposite or whorled — they are "merely approximate by telescoping," and the multiple carpellary traces in Rue Anemone and *Thalictrum* are unlike all other genera in the Ranunculaceae. Furthermore, other species of *Thalictrum* within section *Physocarpum* have subopposite leaves and compact corymbiform inflorescences (Boivin, 1957*b*).

In short, Rue Anemone appears to be an end reduction in an evolutionary lineage featuring alternate leaves and

a non-leafy inflorescence (Boivin, 1957*b*). I concur with Boivin that Rue Anemone does not have sufficiently distinctive characteristics to warrant its separation as a monotypic genus (*Anemonella*), a conclusion also reached by Buchheim (1964), Tamura (1968), Radford (1968), and others.

2. **T. clavatum** DC., Mountain Meadowrue.

Rich moist woods, cliffs, seepage slopes, and mountain streams; mts. and pied. Ga. mts., Ky., N. C., S. C., Tenn., Va. pied., W. Va.

3. **T. mirabile** Small

Moist sandstone bluffs, sinks and rocky crevices, rare. Ala. cp., Ky. mts. and IP, Tenn. IP.

This species is scarcely separable from *Thalictrum clavatum.* Apparently it is more delicate and lax with longer stipes and straight dorsal achene margins. Population studies are needed to assess the comparative differences between this species and *T. clavatum.*

4. **T. dioicum** L. Early Meadowrue.

Rich rocky woods, ravines, and alluvial terraces; chiefly mts. and pied. Ala., Ga. mts., Ky., N. C., S. C., Tenn., Va., W. Va. [Mo., Ill., Ind., Ohio, Pa., N. J.].

5. **T. debile** Buckley

Rich, rocky limestone woods; all prov. Ala., Ga. mts. [Tex.].

6. **T. arkansanum** Boivin

Low grounds and upland woods, rare. Ark. cp.

This species is scarcely separable from *Thalictrum debile.* It is retained as a species pending comparative studies of these two species plus *T. texanum* from central Texas.

7. **T. coriaceum** (Britton) Small

Rich rocky woods; chiefly mts. and pied. Ky. mts., Md. pied., N. C., Tenn. mts., Va., W. Va. Incl. *T. caulophylloides* Small — Small (1933).

Small (1933) characterized *Thalictrum caulophylloides* on the basis of its longer anthers and sepals and more ellipsoid achenes. I am following Boivin (1944) in regarding *T. caulophylloides* as conspecific with *T. coriaceum*, although population studies may show regional morphological differences worthy of taxonomic distinction.

8. **T. steeleanum** Boivin

Moist alluvial thickets, rare; chiefly cp. and pied. Md., Va., W. Va. [Pa.].

This species needs additional study. Apparently it is closely related to *Thalictrum coriaceum*, but *T. steeleanum* differs from this species by its rhizomatous habit, longer anthers and achenes, and the terminal leaflets usually shorter than wide. *T. steeleanum* is usually found in moist alluvial thickets whereas *T. coriaceum* generally grows in rich woods.

9. **T. revolutum** DC.

Dry open woods, brushy banks, thickets, and barrens; all prov. S. E. except La. [Mo., Ill., Ind., Ohio, Pa., N. J.].

The outstanding characteristic of this species is the stipitate-glandular pubescence usually investing both the abaxial surfaces of the leaflets as well as the achenes. No other species of *Thalictrum* in eastern North America has this character. However, occasional specimens lack the stipitate-glandular pubescence, the leaflets then being merely muricate or whitened-papillose beneath. Sometimes such forms (forma *glabra* Pennell, 1931) occasionally have been mistaken for other species (Table II). Usually the petioles and leaf abaxial surfaces of the glabrous forms tend to be glaucous which aids in distinguishing this form of *T. revolutum* from *T. pubescens* and *T. dasycarpum* which usually have puberulent petiolules and leaflets. Anther, sepal, and leaflet size also aid in distinguishing glabrous forms of *T. revolutum* from *T. macrostylum* (Table II). In studying plants belonging to these species (Table II), special care should be given in assessing overall leaflet

Table II. Comparison of Species in the *T. revolutum* — *T. pubescens* Complex.[1]

Character	*T. revolutum*	*T. macrostylum*	*T. pubescens*	*T. dasycarpum*
Leaflets:				
width of largest (mm)	5-40	3-17	15-45	15-45
pubescence	Stipitate-glandular (or muricate to whitish papillose) beneath	Glabrous beneath	± Puberulent with soft trichomes	Minutely puberulent (or glabrous?)
color	Greyish to brownish green	Greyish to brownish green	Usually dark green	Usually dark green
texture	Coriaceous	± Coriaceous to membranous	Membranous to coriaceous	Membranous to firm
margin	Strongly revolute	± Revolute	Revolute to flat	Revolute to flat
Petiolules	Usually glabrous and glaucous	Usually glabrous and glaucous	Usually puberulent	Usually puberulent
Sepal length (mm)	3-4	1-2	2-3.5	3-5
Anther length (mm)	1.5-2.8	0.5-1.2	1.0-1.5	1.5-3.5
Filaments	Slightly clavate, flexuous	Clavate, rigid	Prominently slenderly clavate	± Filiform, flexuous
Stigma length (mm)	2.0-3.5	0.6-1.7	0.5-2.0	2-5
$n =$	ca. 67	—	42, 77	ca. 50
Habitat	Dry open woods, brushy banks, thickets, and barrens	Rich wooded slopes, bluffs, meadows, and limestone sinks	Rich woods, low thickets, swamps, wet meadows, and stream banks	Damp thickets, swamps, and wet meadows
Range in southeastern United States	Throughout	All prov., Va. to S.C., Ala. mts., Miss.	Chiefly pied. and mts., Md. to Ga., Ky., Tenn. and W. Va.	Cp. and mts., Ark. to La.

[1]Based in part on Boivin (1944).

size, color, texture and pubescence, and anther and style length.

10. **T. cooleyi** Ahles

Savannahs, very rare. N.C. cp.

This interesting species, recently described by Ahles (1959), has relatively long, narrow leaflets. Further field work is needed to establish the overall variability of this species.

11. **T. macrostylum** Small & Heller

Rich wooded slopes, bluffs, meadows, and limestone sinks; all prov. Ala. mts., Miss., N.C., S.C., Va. cp.

Characteristically *Thalictrum macrostylum* has small brownish-green coriaceous to membranous glabrous leaflets with generally entire and inrolled margins which amply distinguish this species although glabrous forms of *T. revolutum* may be confused with it. However, such forms of *T. revolutum* usually have larger leaflets, longer anthers, stigmas and sepals, and the filaments tend to be different (Table II).

12. **T. subrotundum** Boivin

Low woods, rare; cp. and pied. Ala., Fla., Ga., S.C.

This species is poorly understood and more field work is needed to establish clearly its identity from *Thalictrum macrostylum*. In general *T. subrotundum* tends to be more lax and taller and its leaves greener and more membranous (Table III). Pending further analysis I am retaining *T. subrotundum* as a species although it may well be a local geographic subspecies of *T. macrostylum*.

13. **T. pubescens** Pursh

Rich woods, low thickets, swamps, wet meadows, and stream banks; chiefly mts. and pied. Ga., Ky. IP, Md., N.C., Tenn., Va., W. Va. [Ind., Ohio, Pa., N.J.]. *T. polygamum* Muhl. — Small (1933), Fernald (1950), Gleason and Cronquist (1963), Radford et al. (1968); incl. *T. perelegans* Green — Small (1933).

No species of *Thalictrum* in our flora has been subject to as much nomenclatural or taxonomic confusion as *T. pubescens.* First, the name appearing in most current manuals is *T. polygamum* Muhl., but this is a *nomen nudum,* Muhlenberg having merely listed it in his *Index Florae Lancastriensis* published in 1793. Later, Sprengel (Syst. Veg. 2: 671. 1825) validated Muhlenberg's name, but by this time, Pursh (1814) had already validly published *T. pubescens.*

Boivin (1957*a*), in reviewing the nomenclature of this species, recognized the priority of *Thalictrum pubescens,* but recommended that *T. polygamum* Muhl. *ex* Sprengel be

Table III. Comparison of *T. macrostylum* and *T. subrotundum.*[1]

Character	*T. macrostylum*	*T. subrotundum*
Height (m)	Up to 1	1-2
Habit	Erect	Lax, ± reclining on adjacent vegetation
Leaflets:		
color	Greyish or brownish green	Green
texture	± Coriaceous	Thin, membranous
margin	Entire to apically 3-lobed	Usually entire
venation	Prominently reticulate beneath	Scarcely reticulate beneath
Filaments	Rigid, distinctly clavate	Weak, scarcely clavate
Stigma length (mm)	ca. 1	1-2
Habitat	Rich wooded slopes, bluffs, meadows, and limestone sinks	Low woods
Range	All prov., Va. to S.C., Ala. mts., Miss.	Cp. and pied., S.C. to Fla. and Ala.

[1]Based in part on Boivin (1944).

conserved in the interest of nomenclatural stability. Despite Boivin's persuasive argument, the present International Code of Botanical Nomenclature (Art. 14) forbids such practice and consequently the earliest correct name (*T. pubescens*) must be used.

Second, *Thalictrum pubescens* is a widespread highly variable species. Its variability is borne out in the work of E. L. Greene who around 1910 described at least thirteen species which according to Boivin (1944) are all taxonomic synonyms referable to *T. pubescens* (= *T. polygamum*).

Table IV. Comparison of *T. pubescens* and *T. dasycarpum*.[1]

Character	*T. pubescens*	*T. dasycarpum*
Inflorescence	± Rounded	± Pointed, pyramidal
Flowers	Usually bisexual	Unisexual
Sepals	Elliptic, rounded	± Lanceolate, acute
Filaments	Clavate, ascending	Filiform, flexuous
Anther length (mm)	0.8-1.5	1.5-3.5
Achenes	Short stipitate	Obtuse at ± sessile base
Stigmas:		
length (mm)	0.5-2.0 (ca. ½ length of achene body)	2-5 (ca. equal to length of achene body)
shape	Sharply curved (like a fiddlehead), with densely matted hairs 0.1 mm long	± Straight, with short hairs 0.05 mm long
Habitat	Rich woods, low thickets, swamps, wet meadows, and stream banks	Damp thickets, swamps, and wet meadows
Range in southeastern U.S.	Chiefly pied. and mts., Md. to Ga., Ky., Tenn., and W. Va.	Cp. and mts., Ark. to La.

[1]Based in part on Boivin (1944).

In *Gray's Manual,* Fernald (1950) recognized three varieties (two occurring outside of the southeastern United States), but Gleason and Cronquist (1963) included only the species. *Thalictrum pubescens* certainly needs study on a population basis throughout its range, but pending such research I prefer to regard it as a single polymorphic species.

Frequently *Thalictrum pubescens* is confused with *T. dasycarpum* and both these species can be confused with *T. coriaceum* and *T. steeleanum,* although with adequate material the distinctions can usually be made (see Tables IV, V).

Table V. Comparison of the *T. coriaceum* Complex with the *T. pubescens* Complex.[1]

Character	*T. coriaceum* and *T. steeleanum*	*T. pubescens* and *T. dasycarpum*
Leaflets:		
lobe number	3	0-3
lobe margin	Crenate	Entire
pubescence	Usually glabrous beneath	± Puberulent beneath
Stipes:		
length (mm)	0.5-3.0	0-1
cross-section	± Wing-angled	± Terete
Filaments	Filiform, colored	± Clavate, white
Anther length (mm)	2-4 (in *T. coriaceum*) 3.5-4.4 (in *T. steeleanum*)	0.8-1.5 (in *T. polygamum*); 1.5-3.5 (in *T. dasycarpum*, an infrequent species)

[1]Based in part on Boivin (1944).

14. **T. dasycarpum** Fischer & Avé-Lall., Purple Meadowrue. Damp thickets, swamps, and wet meadows; cp. and mts. Ark., La., Miss. [Tex., Okla., Mo., Ill., Ind., Ohio, Pa.].

Thalictrum dasycarpum is apparently closely related to *T. pubescens,* although mature specimens can usually be

distinguished (Table IV). Nevertheless, *T. dasycarpum* is a similarly variable species in need of further study. Between 1909 and 1912 Greene described at least six species which according to Boivin (1944) are all taxonomic synonyms of *T. dasycarpum*. More recently, Rydberg (1931) described plants from Texas and Kansas (*T. hypoglaucum*) which he stated were similar to *T. dasycarpum* but differed by having glabrous leaves and smaller, glabrous achenes. Although Boivin (1944) later reduced *T. hypoglaucum* to a variety under *T. dasycarpum*, the taxonomic status and relationship of this taxon remains in doubt. For example, glabrous forms of both *T. revolutum* and *T. dasycarpum* ("var. *hypoglaucum*") are difficult to distinguish (see Steyermark, 1963, p. 675), and further study is needed to clarify the taxonomic relationship.

Pending further work, I am regarding *Thalictrum dasycarpum* as a polymorphic species occurring chiefly in the central to northwestern United States and adjacent Canada, but which is infrequent within the southeastern United States.

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LITERATURE CITED

AHLES, H. E. 1959. *Thalictrum cooleyi* sp. nov. Brittonia **11**: 68-70.

BOIVIN, B. 1944. American Thalictra and their Old World allies. Rhodora **46**: 337-377, 391-445, 453-487.

———. 1957*a*. Études thalictrologiques. II. *Thalictrum polygamum* Muhlenberg, nomen specificum conserva[n]dum. Bull. Soc. Bot. Belg. **89**: 315-318.

———. 1957*b*. Études thalictrologiques. III. Réduction du genre *Anemonella* Spach (Ranunculaceae). Bull. Soc. Bot. Belg. **89**: 319-321.

BRITTON, N. L. 1891. The American species of the genus *Anemone* and the genera which have been referred to it. Ann. N.Y. Acad. Sci. **6**: 215-238.

BUCHHEIM, G. 1964. Ranunculaceae, p. 133-137. *In* H. Melchior (ed.). A. Engler's Syllabus der Pflanzenfamilien, Band II, Auflage 12. Gebrüder Borntraeger, Berlin-Nikolassee.

CAVE, M. S. (ed.). 1962. Index to plant chromosome numbers for 1961, Vol. II(6): 119. Univ. of North Carolina Press, Chapel Hill.

DAVIS, D. C. 1900. A synonymic conspectus of the native and garden Thalictrums of North America. Minn. Bot. Stud. **2**: 509-523.

FERNALD, M. L. 1950. Gray's manual of botany, 8th ed. American Book Co., New York.

GLEASON, H. A. & A. CRONQUIST. 1963. Manual of vascular plants of northeastern United States and adjacent Canada. D. Van Nostrand, Princeton, N.J.

GRAY, A. 1895. Ranunculaceae, p. 1-57. *In* B. L. Robinson (ed.), Synoptical flora of North America, Vol. I, pt. 1. American Book Co., New York.

————. 1886. *Anemonella thalictroides* Spach, Hist. Nat. Veg. vii. 239. Bot. Gaz. **11**: 39.

GREGORY, W. C. 1941. Phylogenetic and cytological studies in the Ranunculaceae. Trans. Amer. Phil. Soc., N.S. **31**(pt. 5): 441-521.

JENSEN, H. W. 1944. Heterochromosome formation in the genus *Ilex*. Amer. Nat. **78**: 375-379.

KAPLAN, S. M., & D. L. MULCAHY. 1971. Mode of pollination and floral sexuality in *Thalictrum*. Evolution **25**: 659-668.

KUHN, E. 1928. Zur Zytologie von *Thalictrum*. Jahr. Wiss. Bot. **68**: 382-430.

LECOYER, J. -C. 1885. Monographie du genre *Thalictrum*. Bull. Soc. Bot. Belg. **24**: 78-324.

LÖVE, A. & D. LÖVE. 1966. Cytotaxonomy of the alpine vascular plants of Mount Washington. Univ. Colorado Studies, Ser. Biol. **24**: 1-74.

MUHLENBERG, H. 1793. Index Florae Lancastriensis. Trans. Amer. Phil. Soc. **3**: 157-184.

ORNDUFF, R. (ed.). 1968. Index to plant chromosome numbers for 1966. Reg. Veg. **55**: 54.

————. 1969. Index to plant chromosome numbers for 1967. Reg. Veg. **59**: 56.

PENNELL, F. W. 1929-1930 [1931]. On some critical species of the serpentine barrens. Bartonia **12**: 1-23.

PURSH, F. 1814. Flora americae septentrionalis. London.

RADFORD, A. E. 1968. Ranunculaceae, p. 452-468. *In* A. E. Radford, H. E. Ahles, & C. R. Bell, Manual of the vascular flora of the Carolinas. Univ. of North Carolina Press, Chapel Hill, N.C.

————, C. R. BELL, J. W. HARDIN, & R. L. WILBUR. 1967. Contributor's guide for the vascular flora of the southeastern United States. Dept. of Botany, Univ. of North Carolina, Chapel Hill, N.C.

SMALL, J. K. 1933. Manual of the Southeastern flora. Publ. by the author, New York.

SOROKIN, H. 1929. Idiograms, nucleoli and satellites of certain Ranunculaceae. Amer. J. Bot. **16**: 407-420.

STEYERMARK, J. A. 1963. Flora of Missouri. The Iowa State Univ. Press, Ames, Iowa.

TAMURA, M. 1968. Morphology, ecology and phylogeny of the Ranunculaceae. VIII. Sci. Rep. Osaka Univ. **17(1)**: 41-56.

TORREY, J. & A. GRAY. 1838. A flora of North America, Vol. 1. Wiley & Putnam, New York. [Facsimile edition, 1969. Hafner Publ. Co., New York.].

TRELEASE, W. 1886. North American species of *Thalictrum*. Proc. Bost. Soc. Nat. Hist. **23**: 293-304.

ZHUKOVA, P. G. 1961. Studies in the caryology of some species of Ranunculaceae in the Arcto-Alpine Botanic Garden of the Kola Branch of the Academy of Sciences of the U.S.S.R. (Kola Peninsula). Bot. Zhur. SSSR **46**: 421-428.

————. 1967. Karyology of some plants, cultivated in the Arctic-alpine Botanical Garden (In Russian), p. 139-149. *In* N. A. Avrorin (ed.), Plantarum in Zonam Polarem Transportatio. II. Leningrad.

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DISPERSION OF FERN SPORES INTO AND WITHIN A FOREST[1]

GILBERT S. RAYNOR, EUGENE C. OGDEN AND JANET V. HAYES

Experiments were conducted at Brookhaven National Laboratory over a nine-year period to study the spread by atmospheric dispersion of small particles released within and upwind of a forest. Most particles utilized were pollens and spores selected for a range of sizes. One hundred nineteen releases were made in forty-two separate experiments. Ragweed (*Ambrosia*) pollen was studied most extensively and may be considered a reference particle to which other tracers can be compared. Spores of ferns (*Osmunda* and *Dryopteris*) were released in four tests and, in each case, ragweed pollen was released simultaneously from the same location. This paper describes the dispersion of these fern spores and compares it to the dispersion of ragweed pollen. The forest dispersion studies and their results have been reported previously but without detailed consideration of the fern spore releases (Raynor, *et al.*, 1972, 1974a, 1974b, 1975).

SITE

Experiments were conducted in a forest composed largely of Red Pine (*Pinus resinosa*) with smaller amounts of White Pine (*P. strobus*), Pitch Pine (*P. rigida*) and several deciduous species. Average tree height increased from about 10.5 to 13.0 m during the experimental years. The stand is rather dense with 1474 trees per hectare. The canopy is mostly closed but numerous small openings are

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present. The forest has a straight edge in an east-west direction with an open field to the south. Except at the edge where dense foliage extends to the surface, little living foliage is present below 2 to 4 m. Sparse undergrowth is present only in a few clearings. More detailed descriptions of the site with illustrations were given earlier (Raynor, 1971; Raynor *et al.*, 1972).

EQUIPMENT AND METHODS

The sampling network was composed of 119 rotoslide samplers (Ogden and Raynor, 1967) mounted at heights from 0.5 to 21.0 m on towers and other supports along seven rows, 10 m apart, extending from just outside the forest edge to 100 m into the forest at right angles to the edge. These samplers rotate at about 1500 revolutions per minute and collect particles by impaction on the edges of two microscope slides. The edges are coated with silicone grease to insure retention of impacted particles. Deposition to the ground was measured by two greased microscope slides at each of the 57 sampling locations.

Meteorological conditions at the experimental site were measured by 25 sensitive cup anemometers mounted in and near the forest at heights from 1.75 to 21.0 m and by 10 aspirated temperature sensors mounted at selected heights in the forest and the field. Other measurements were taken at a nearby meteorological installation.

The micrometeorology of the forest was described earlier (Raynor, 1971) but is summarized briefly here. With a long fetch through the forest, wind speeds below the canopy are very light compared to those in the open and vary little from near the ground to mid-canopy where an increase takes place. When winds penetrate the edge from the field, speeds are greater in the trunk space than in the canopy for a distance of about 60 m. When unstable lapse rates are present outside the forest, a temperature inversion or an isothermal layer is typical below the canopy. The vertical component of turbulence is more pronounced and the lateral component less so than in the open.

Particles used as tracers were previously purchased or collected, suspended in a liquid and sprayed out through compressed-air-operated atomizing nozzles (Raynor and Smith, 1964). Pollens were prestained with selected colors (Raynor, *et al.*, 1966) to facilitate identification and counting but the darker spores did not absorb the stains used and were identified after collection by size, shape and surface characteristics. Ragweed pollen is spheroidal, rough and about 20 μm in diameter. *Osmunda* spores are also spheroidal but smooth and average about 54 μm in diameter. *Dryopteris* spores are ovoidal, slightly rough and average about 33 × 45 μm.

In preparation for an experiment, the selected quantity of particles was weighed on a laboratory balance, mixed in a liquid and both stirred and agitated ultrasonically to separate clumps. When pollens were used, the dye was added to the liquid at this stage. When well mixed, the suspension was placed in the dispensing apparatus at the selected release point. Mixing continued during the release period which usually lasted from 20 to 40 minutes. Slides were placed in the samplers and at the deposition sites shortly before emission. Rotoslide samplers were started before release began and operated until after the spray terminated. In most tests, releases of the same particle type were made from three locations simultaneously but, in others, several particle types were emitted from the same location. After each test, slides were collected and stored for later analysis. Each type of particle or each color of pollen used was counted separately on each slide by use of a microscope.

The count data were normalized by the volume of air sampled and by the sampler efficiency to give concentrations in particles/m^3 of air sampled. Deposition data were expressed as particles/m^2 of ground surface. No measurement was obtained of particles which impacted or deposited on the vegetation. Since the number of particles/gram had previously been determined for each species, the number of particles released in each test was calculated. Therefore,

all concentration and deposition data were further normalized by the output rate so that these parameters were expressed as percentages of the total output. This allowed direct comparison of results between tests since amounts released varied from one test or one particle type to another. The data were then analyzed in various ways to determine the rate and character of dispersion and the rate of particle loss from the air.

More complete descriptions of the equipment and methods used were given earlier (Raynor, *et al.*, 1966, 1972, 1974a, 1974b, 1975).

RESULTS

Since only four tests were made using fern spores, these are described separately and results compared directly to results from simultaneous ragweed pollen releases. Since the fern spore data were too few for certain analyses performed on the more complete pollen data, only selected analyses are discussed here. However, these are adequate to characterize the results found and to indicate the behavior of fern spores under the conditions of the experiments.

In test 30, *Osmunda* spores and ragweed pollen were released from a height of 1.75 m at a point in the field 15 m upwind of the forest edge. The normalized concentration patterns at the 1.75 m height are shown in Figure 1a and are qualitatively similar. Mean wind speed was 2.3 m/sec. at the release point, adequate for good penetration into the forest edge. As found for upwind releases in general (Raynor, *et al.*, 1974b) the plumes widen greatly before the edge is reached due to increased turbulence in this region, but additional lateral spread within the forest is small. The fern spore pattern is more irregular, probably due to two factors: 1) the smaller number of particles emitted with consequent smaller and less reliable counts and 2) more rapid removal by impaction and deposition at

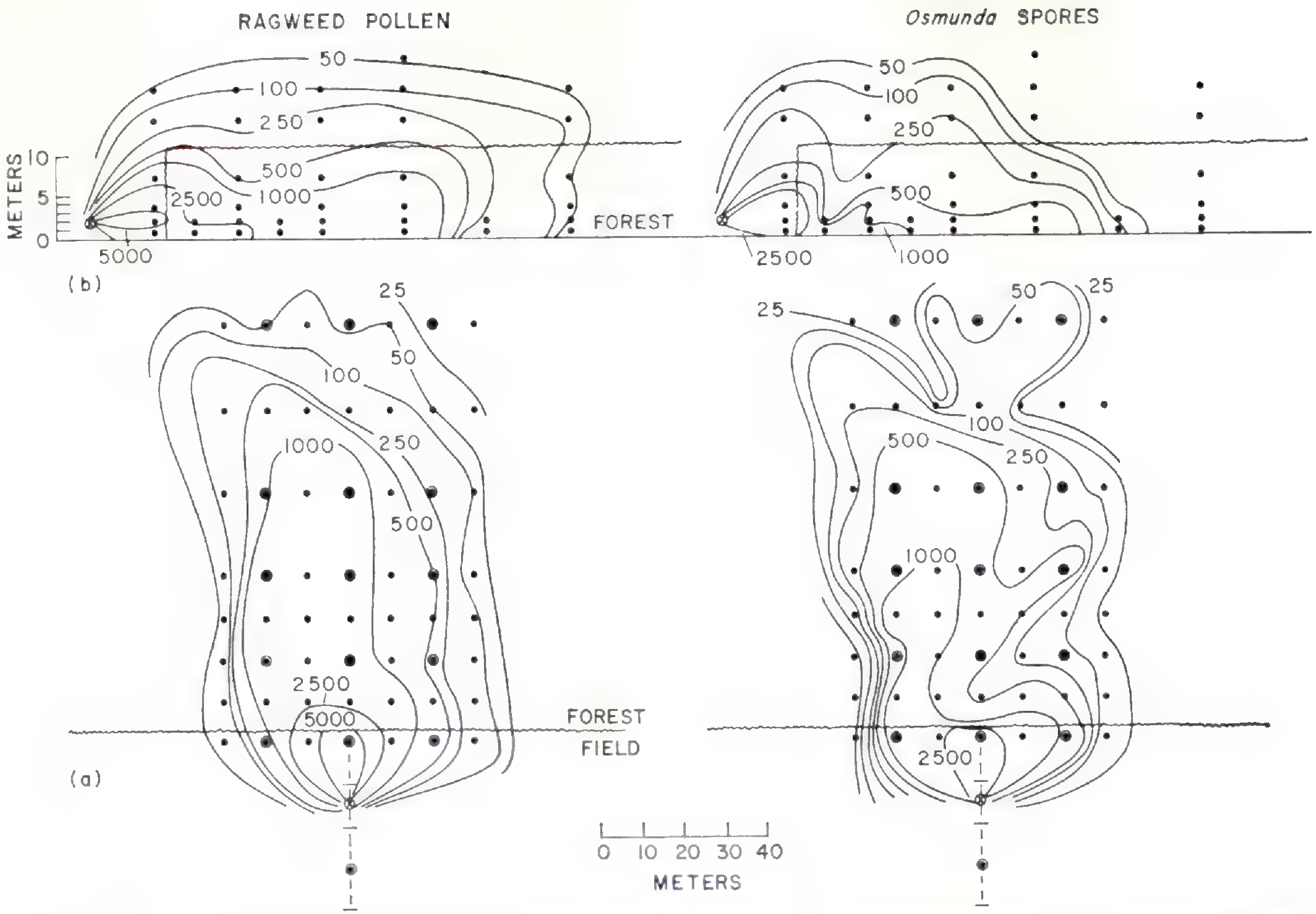

Figure 1. Concentration isopleth patterns resulting from simultaneous releases of ragweed pollen and *Osmunda* spores at a height of 1.75 m, 15 m upwind of the forest edge. Test 30. (a) horizontal plane at a height of 1.75 m. (b) downwind-vertical plane along the grid centerline.

locations in the forest where local foliage distribution and wind flow patterns favored these processes. For both particles, maximum concentrations are found to the left of the centerline of the sampling grid, apparently due to channelling of the air by variations in foliage density.

Figure 1b shows vertical cross sections along the downwind centerline of the sampling grid. Although some of both particles were carried up over the forest at the edge, the concentration isopleths of the *Osmunda* spores slope down at 60 m in the forest whereas those of the ragweed pollen remain nearly horizontal to the most distant sampling location. This effect is due to more rapid settling and removal of the larger fern spores.

In test 40, *Dryopteris* spores and ragweed pollen were released simultaneously from a height of 1.75 m at a location 95 m in the forest with the wind blowing through the forest towards the field. As shown in Figure 2a, concentrations of *Dryopteris* spores decreased much more rapidly with distance than concentrations of ragweed pollen, again due to the greater loss of the larger fern spores. Mean wind speed was only 0.4 m/sec. at the release point so the clouds of particles moved slowly through the forest with ample time for settling to the ground and to the foliage.

Figure 2b shows the downwind cross section along the grid centerline. The lesser height reached by comparable concentrations of fern spores and the more rapid decrease with distance are evident.

In test 26, *Osmunda* spores and ragweed pollen were emitted together from a height of 1.75 m, 100 m in the forest. Wind speed was again 0.4 m/sec. at the release point but somewhat less above the forest than in test 40. Concentrations of *Osmunda* spores (Figure 3) decreased very rapidly with distance and became negligible in about 40 m while concentrations of ragweed pollen remained appreciable to the forest edge at 100 m. The vertical patterns are not shown since the fern spores remained low within the forest.

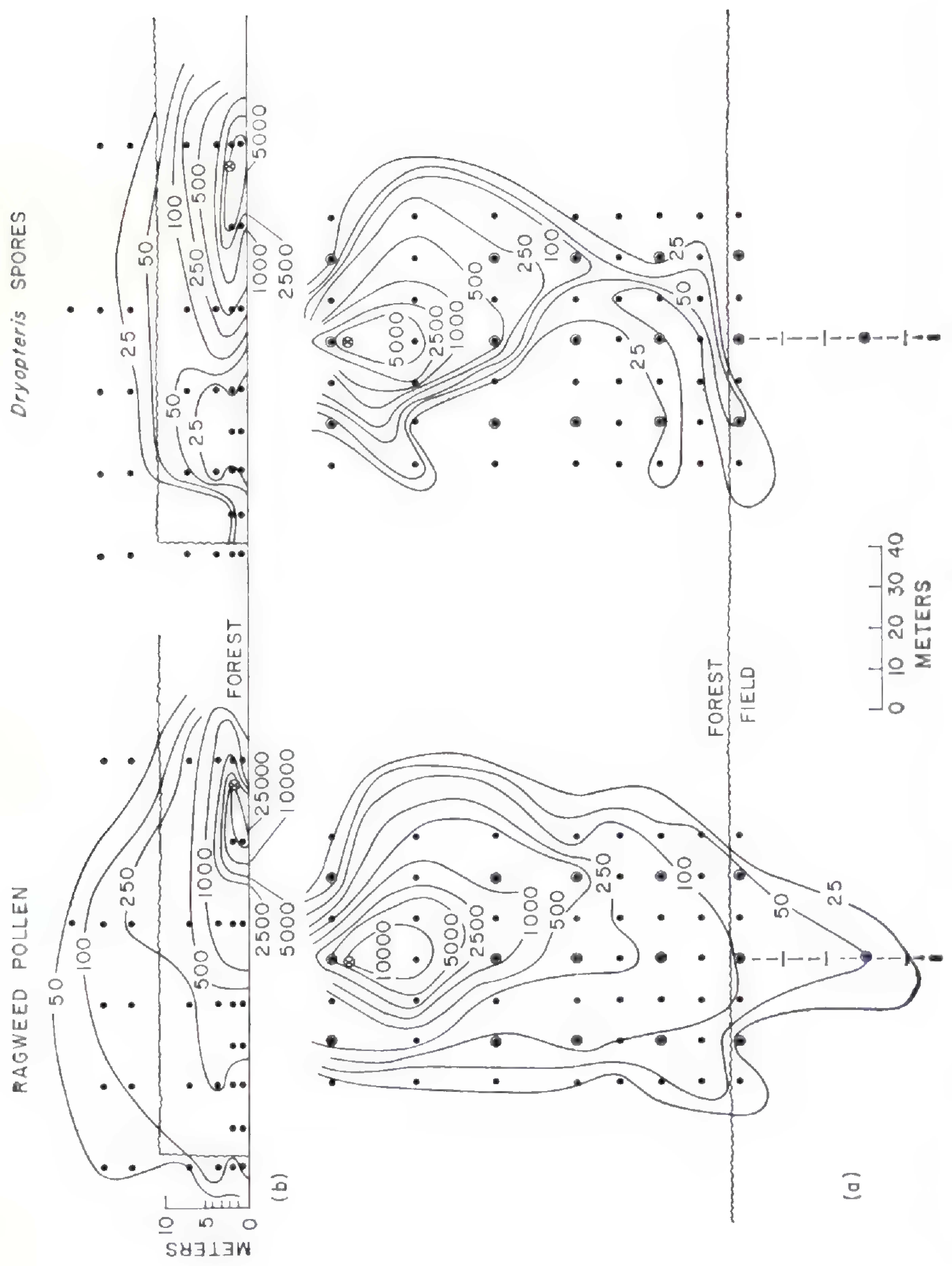

Figure 2. Concentration isopleth patterns resulting from simultaneous releases of ragweed pollen and *Dryopteris* spores at a height of 1.75 m, 95 m in the forest. Test 40. (a) horizontal plane at a height of 1.75 m. (b) downwind-vertical plane along the grid centerline.

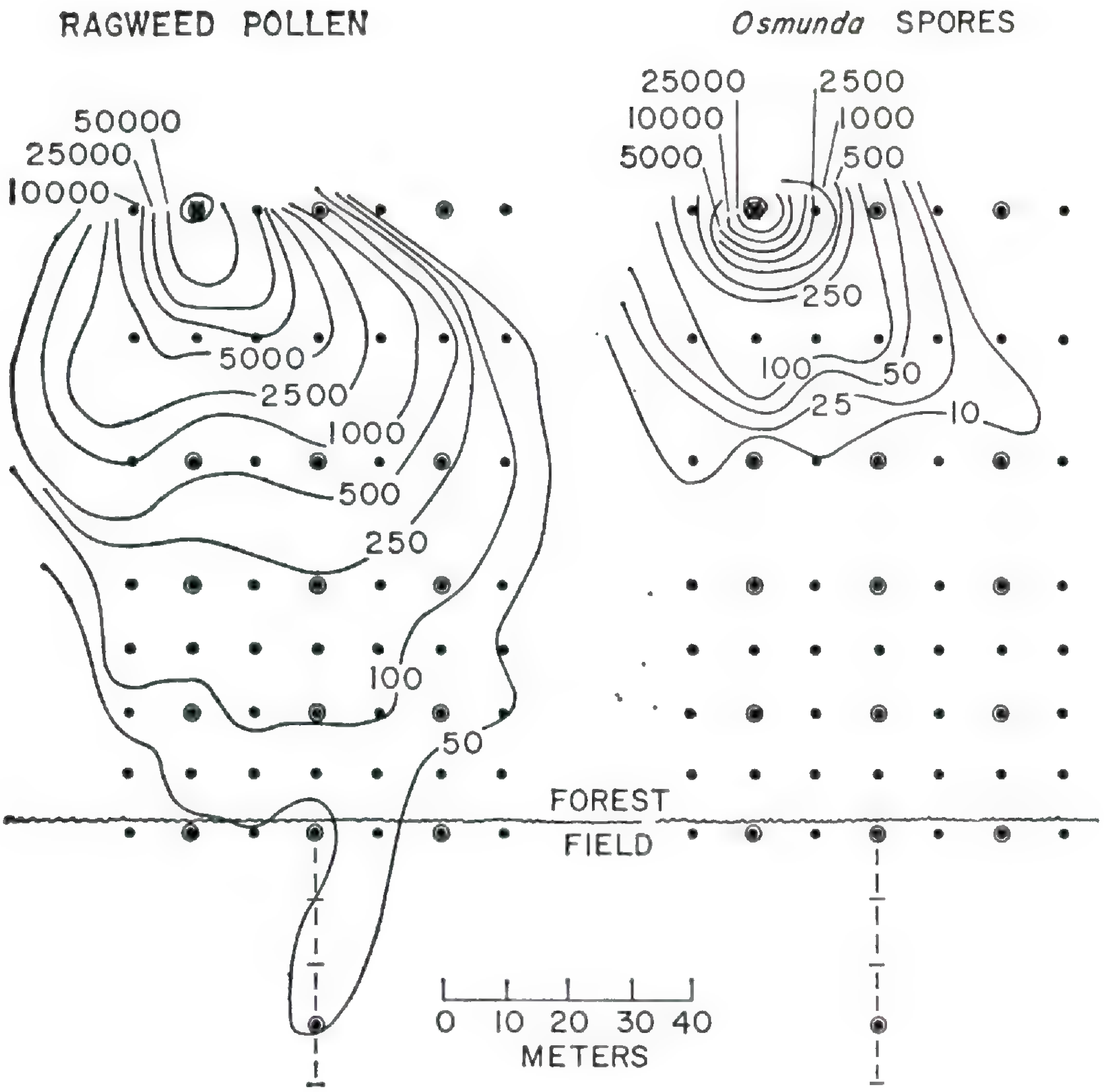

Figure 3. Concentration isopleth patterns in the horizontal plane at a height of 1.75 m resulting from simultaneous releases of ragweed pollen and *Osmunda* spores at a height of 1.75 m, 100 m in the forest. Test 26.

Nearly identical results were obtained in test 32 when the same particles were released at the same height 95 m in the forest. Wind speed at the release point was only about 0.1 m/sec. and that above the forest at a height of 14 m only 1.4 m/sec. Thus, wind directions were variable and many of the particles were transported to the northwest and out of the sampling grid instead of to the south as had been expected (Figure 4). However, it is obvious that the *Osmunda* spores were lost from the air in a very short distance in contrast to the ragweed pollen.

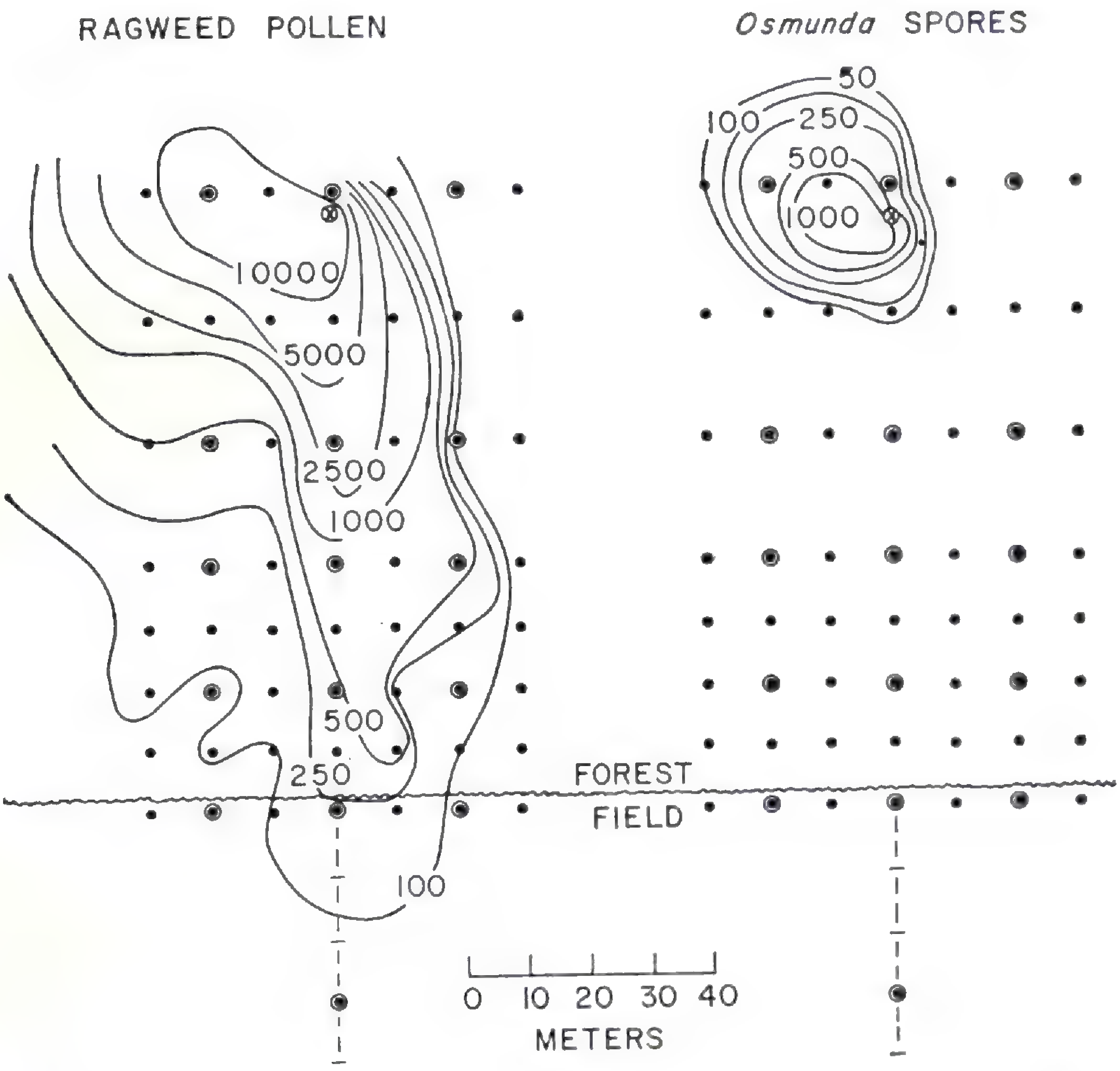

Figure 4. Concentration isopleth patterns in the horizontal plane at a height of 1.75 m resulting from simultaneous releases of ragweed pollen and *Osmunda* spores at a height of 1.75 m, 95 m in the forest. Test 32.

Centerline concentrations at the 1.75 m level were normalized to 100% at the edge of the forest and plotted as a function of distance within the forest (Figure 5). Except for greater irregularity in the *Osmunda* curve (B) rate of loss was not significantly different than for ragweed pollen (A).

The concentration data were then integrated in all three coordinate directions to give the mass flux or the total number of particles remaining airborne at each distance. These data are also plotted relative to the values at the

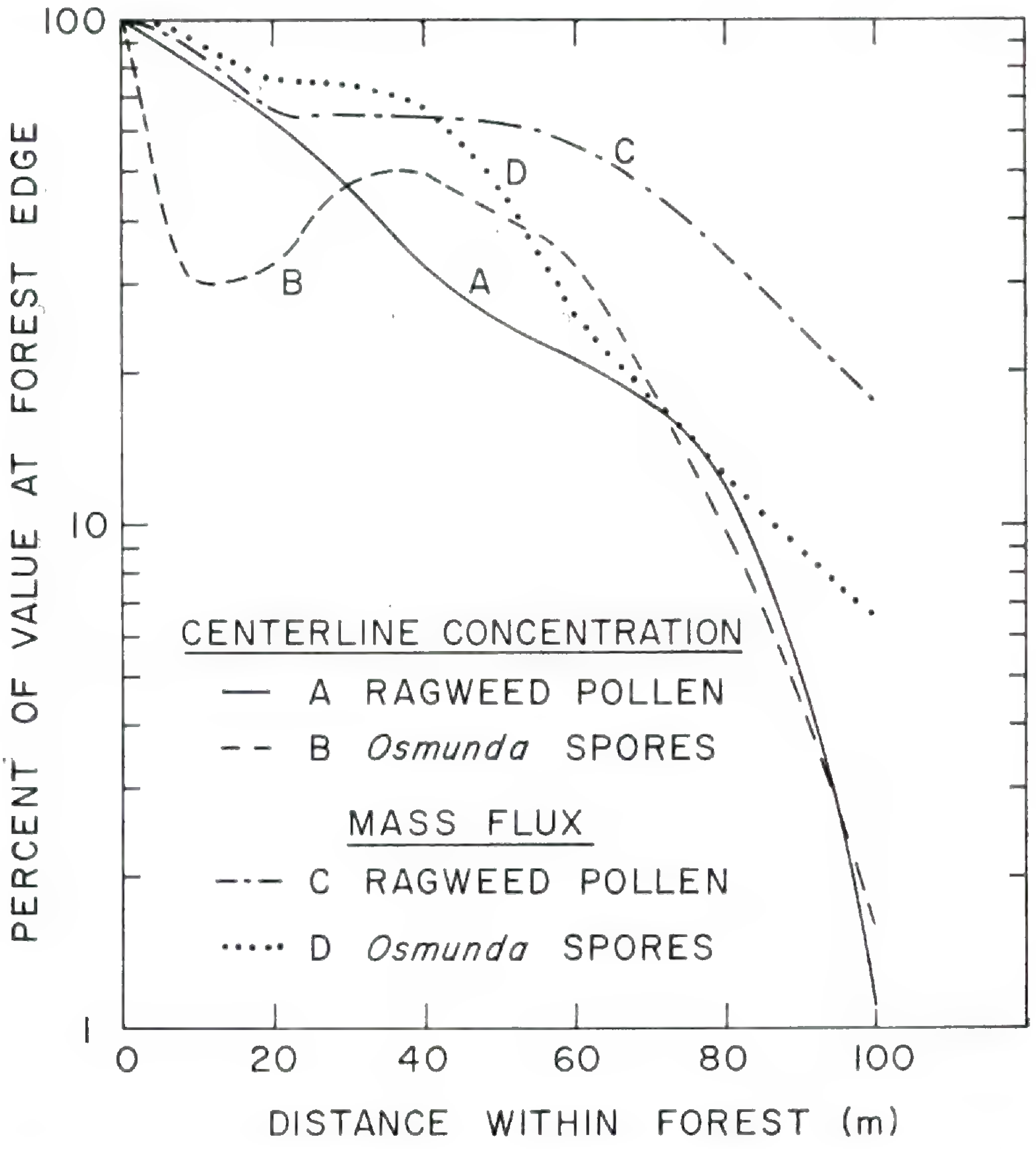

Figure 5. Normalized centerline concentrations and mass flux as a function of distance within the forest for simultaneous releases of ragweed pollen and *Osmunda* spores upwind of the forest edge. Test 30.

edge of the forest in Figure 5. Here, it is seen that the *Osmunda* spores (D) are lost appreciably faster than the pollen grains (C) so that at 100 m, nearly three times as many pollen grains remain airborne.

Deposition to the ground of the two particles is compared in a similar way in Figure 6. Since centerline deposition was typically irregular, deposition integrated in the crosswind direction across the width of the deposition

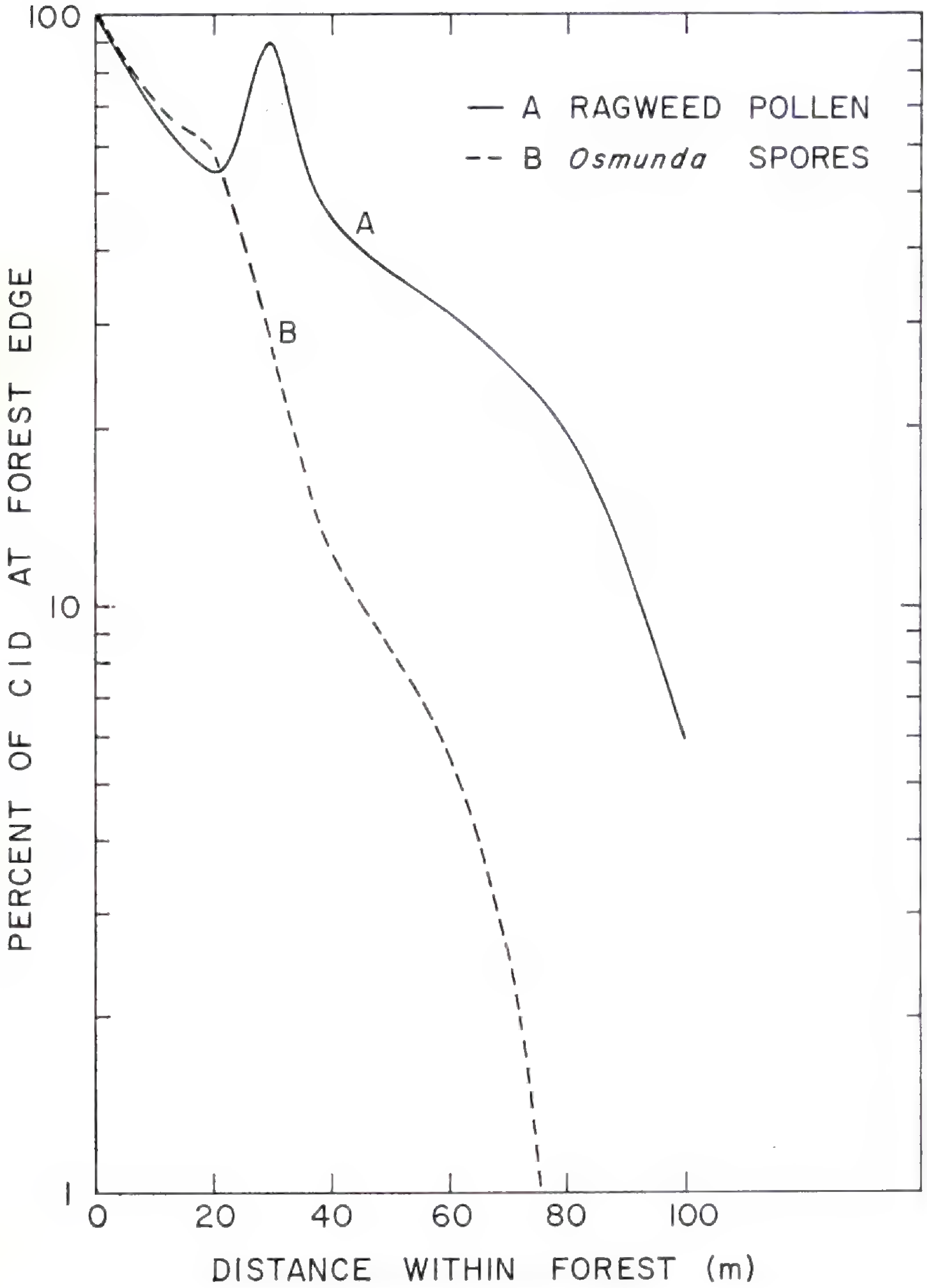

Figure 6. Normalized crosswind integrated deposition as a function of distance within the forest for simultaneous releases of ragweed pollen and *Osmunda* spores upwind of the forest edge. Test 30.

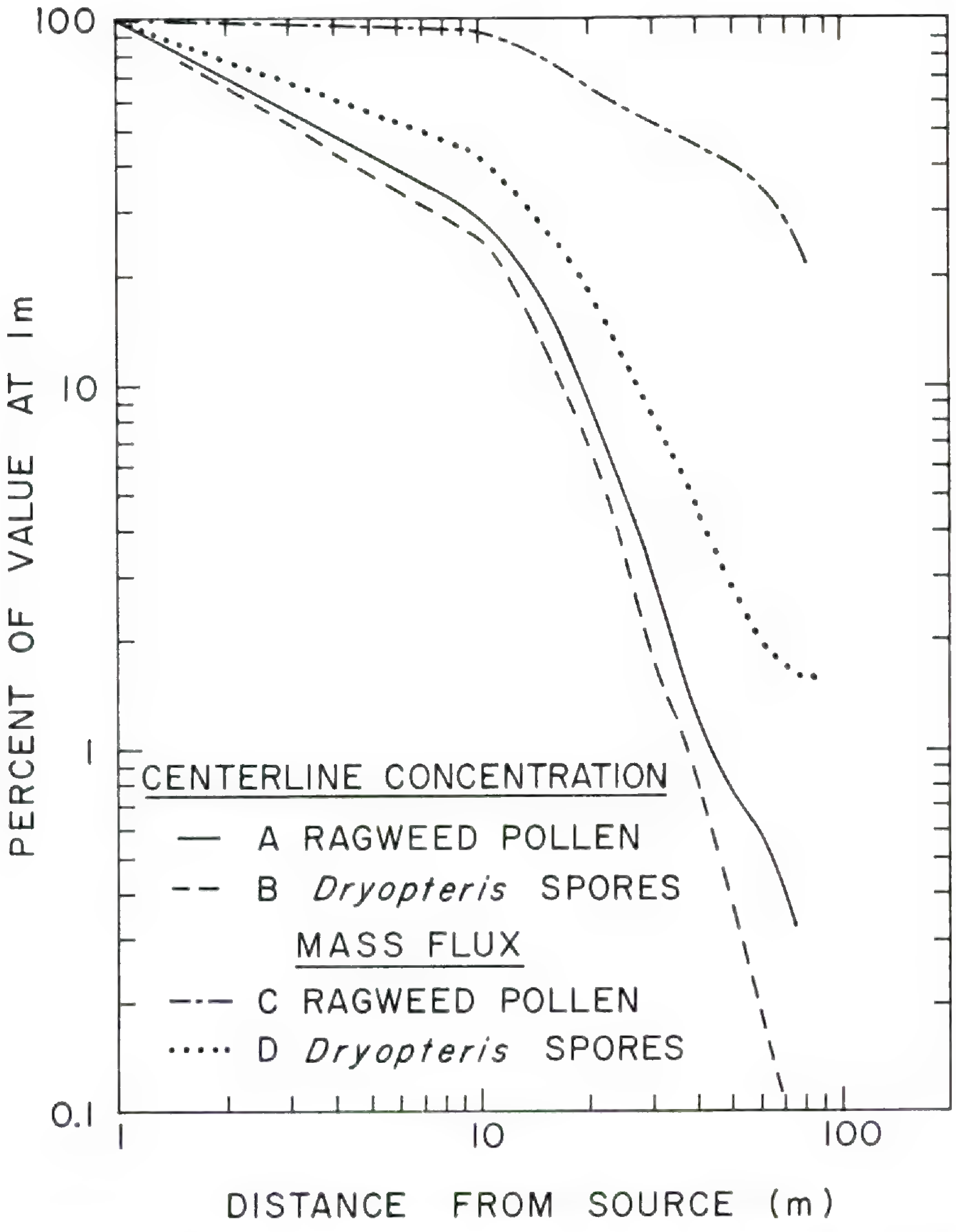

Figure 7. Normalized centerline concentrations and mass flux as a function of distance from the source for simultaneous releases of ragweed pollen and *Dryopteris* spores within the forest. Test 40.

pattern is shown instead. This is termed crosswind integrated deposition (CID). Decreases in the amounts deposited are similar for the first 20 m but much more rapid thereafter for the *Osmunda* spores.

Changes in centerline concentration and mass flux with

distance from the source are shown in Figure 7 for the *Dryopteris* spores and ragweed pollen released within the forest in test 40. Centerline concentration decreased only slightly more rapidly for the spores (B) than for the pollen (A). However, the total number of grains remaining airborne was much less for the *Dryopteris* spores than for the ragweed pollen at all distances. At 80 m, more than

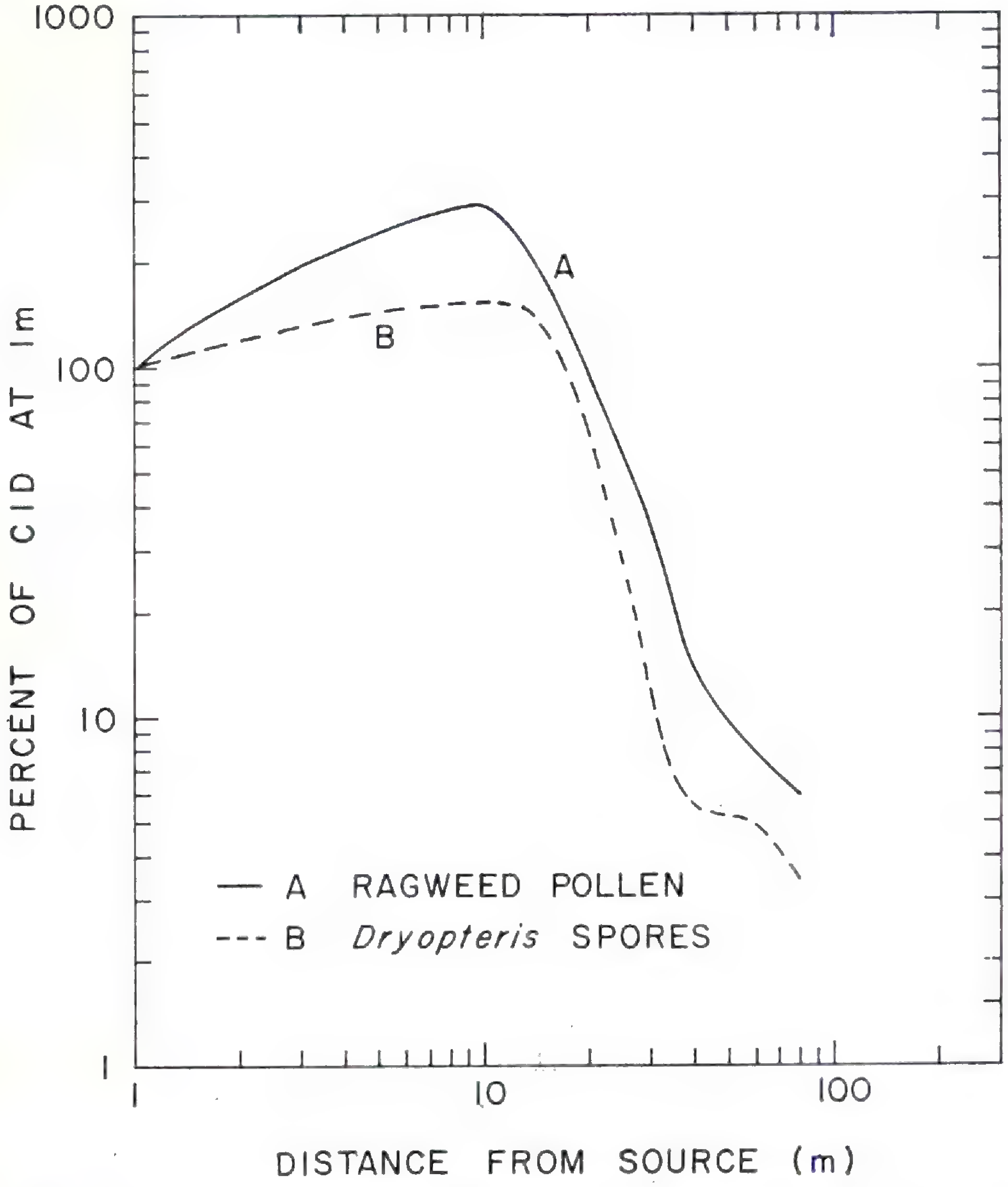

Figure 8. Normalized crosswind integrated deposition (CID) as a function of distance from the source for simultaneous releases of ragweed pollen and *Dryopteris* spores within the forest. Test 40.

10 times as many pollen grains were still airborne than fern spores.

In Figure 8, crosswind integrated deposition to the ground is illustrated for the same test. Here, differences are not as great but fern spore deposition falls off more rapidly than deposition of ragweed pollen. Peak deposition of both species is at 10-12 m from the source which is typical for a source at this height.

DISCUSSION AND CONCLUSIONS

Results indicate that fern spores of the sizes studied are dispersed by atmospheric motions in a manner qualitatively similar to smaller particles but are lost from the atmosphere faster due to their larger size and greater gravitational settling velocity. This agrees with conclusions reached from more extensive studies of particles having a wider range of sizes.

Use of quantitative measurements obtained in these tests to predict fern spore dispersion under natural conditions is difficult since vegetative, topographic and meteorological conditions will seldom be similar. However, certain generalities are evident. Spores of ferns growing in the open will be dispersed more widely and travel greater average distances than spores of ferns growing within forests. In most situations, travel distance and the length of time spores remain airborne will increase with increasing wind speed. Most spores released will settle to the ground or to other vegetation within relatively short distances, but a few may be carried long distances, particularly during periods of strong winds and good atmospheric mixing. The wide distribution of some fern species, and especially the occurrence of ferns on isolated oceanic islands (Tryon, 1970) indicate a capacity for dispersal over long distances, but probably only during exceptionally favorable circumstances. More would have to be known about the meteorological conditions under which fern spores are released naturally to attempt more quantitative predictions.

ACKNOWLEDGEMENTS

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LITERATURE CITED

OGDEN, E. C., & G. S. RAYNOR. 1967. A new sampler for airborne pollen: the rotoslide. J. Allergy **40**: 1-11.

RAYNOR, G. S. 1971. Wind and temperature structure in a coniferous forest and a contiguous field. Forest Sci. **17**: 351-363.

RAYNOR, G. S., L. A. COHEN, J. V. HAYES, & E. C. OGDEN. 1966. Dyed pollen grains and spores as tracers in dispersion and deposition studies. J. Appl. Meteor. **5**: 728-729.

RAYNOR, G. S., J. V. HAYES, & E. C. OGDEN. 1972. Experimental data on particulate dispersion into and within a forest. Part I. Dispersion from upwind point sources. Informal report BNL 17750, Brookhaven National Laboratory, Upton, N. Y. 95 p.

————. 1974a. Experimental data on particulate dispersion into and within a forest. Part III. Dispersion from sources within and above the forest. Informal report BNL 19474, Brookhaven National Laboratory, Upton, New York, 48 p.

————. 1974b. Particulate dispersion into and within a forest. Boundary-layer Meteor. **7**: 429-456.

————. 1975. Particulate dispersion from sources within a forest. Boundary-layer Meteor. **9**: 257-277.

RAYNOR, G. S., & M. E. SMITH. 1964. A diffusion-deposition tracer system. Report BNL 859 (T-343), Brookhaven National Laboratory, Upton, New York, 17 p.

TRYON, R. 1970. Development and evolution of fern floras of oceanic islands. Biotropica **2**: 76-84.

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STUDIES ON THE STELLARIA LONGIPES GOLDIE COMPLEX — VARIATION IN WILD POPULATIONS[1]

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Stellaria longipes Goldie *s.l.* is a very variable species of circumpolar distribution (see map in Chinnappa and Morton, 1974) and wide ecological amplitude. These factors have led previous workers to describe and name many species and varieties within the complex (e.g., Hultén, 1943; Böcher, 1951; Porsild, 1963). However, identification of both living and herbarium material is frequently difficult and uncertain, and the taxa appear not to be clearly differentiated. Other workers (e.g., Polunin, 1959; Anderson, 1959; and Raup, 1947) recognise a single variable species. Cytologically the species is very variable, displaying both euploidy and aneuploidy, with diploid chromosome numbers ranging from 51 to 107; 52, 78 and 104 are the most frequent. There is no correlation between chromosome number and taxonomy (Chinnappa and Morton, 1974; Philipp, 1972). The purpose of the present paper is to explore the range of morphological variation in this species complex, the geographical distribution of this variation and the extent to which the characters are correlated in a manner which might justify the recognition of taxa. We have confined this study to material from North America, a region containing all the main variational trends, and one in which the species complex is most highly developed, widely distributed, and abundant.

MATERIALS AND METHODS

This study is based on material in several of the major North American herbaria (CAN, DAO, TRT, GH) and in the writers' own collections. Over 1500 specimens have been

[1]Based on part of a thesis (Chinnappa, 1973) submitted to the University of Waterloo in partial fulfillment of the requirements for the degree of Ph.D.

examined. The extensive collections in CAN, largely built up by Dr. Porsild for his study of this complex (Porsild, 1963) proved of particular value. The material we have examined came from the whole of the range of the species in North America and contains all the known variational trends and cytotypes. Material from outside North America was also examined, but was not included in the statistics. It shows no significant differences from that found in North America. For reasons of space, the collections studied, and the basic data obtained from them, are not listed in this account.

The characters used in this study include all those regarded as being of taxonomic significance by previous workers. Many of these characters, such as pubescence, and the development of scarious bracts, do not lend themselves to numerical assessment. Pictorial scatter diagrams (a method developed by Anderson, 1949), are a particularly useful means of presenting this type of data, and they provide an effective and concise visual method of demonstrating correlation between characters, or between characters and geographical distribution. Flower size and petal shape are not readily studied in herbarium specimens and were excluded from the present study. Many herbarium specimens do not bear capsules or seeds, due either to their immaturity when collected, or to the adverse climatic conditions under which the plants were growing. This is particularly so in material from the high arctic where the severe climate often damages the developing anthers or curtails the flowering season.

RESULTS

The following are the characters studied in this investigation:

Habit. This ranges from short, compact cushion-like plants found mainly in the arctic, to tall or diffuse plants, or ones with creeping underground stems. The last are often associated with unstable terrain such as gravel slopes and screes. The length of flowering shoots ranges from 2 to

40 cm. with the shorter plants found mainly in the arctic and in the mountain ranges to the south. Two of the extremes are represented by *Stellaria crassipes* Hult. with a compact cushion habit and short flowering shoots, and by *S. arenicola* Raup with long, straggling, diffuse stems, spreading from a central caudex. Mean internode length (see Fig. 1A) was determined by measuring the middle internode on 2 representative mature flowering shoots from each plant. It provides a partial measure of habit, though it does not indicate whether plants are straggling, creeping or erect.

Inflorescence. The number of flowers in the inflorescence varies greatly and ranges from one to many. The mean number was determined for each plant. For purposes of the pictorial scatter diagrams, plants were classified into four inflorescence types:

Type 1. 1-flowered (occasionally 2)
Type 2. 3-flowered (an occasional inflorescence may have more)
Type 3. few-flowered (2-7 flowers) mean 4.5
Type 4. many-flowered (more than 7) mean 10.0

Types 1 and 2 were predominantly associated with *Stellaria monantha* Hultén, *S. laeta* Richards and *S. crassipes* Hultén, types 3 and 4 with *S. longipes* Goldie, *S. stricta* Richards, *S. arenicola* Raup, *S. subvestita* Greene, *S. Edwardsii* R. Br. and *S. Laxmanni* Fisch. These four inflorescence types were fairly evenly represented in the material we examined, their percentage occurrence being 26.1, 27.1, 26.5 and 20.3 respectively.

The presence and absence of scarious bracts in the inflorescence has been considered to be an important taxonomic character by most students of this complex. Plants without scarious bracts have been described as *Stellaria monantha* (when glabrous) and *S. laeta* (when pubescent). Our observations show that 74.25% of the plants we examined had scarious bracts, which were absent in the remainder.

Capsule. Capsule length ranges from 3 to 8 mm. but is usually from 4.5 to 6.5 mm. (Fig. 1B). Capsules always exceed the calyx in length. There is a gradation in capsule colour from straw-coloured through pale brown and brown to black. Straw-coloured capsules are of rare occurrence in most areas, whilst black ones predominate (Fig. 1C).

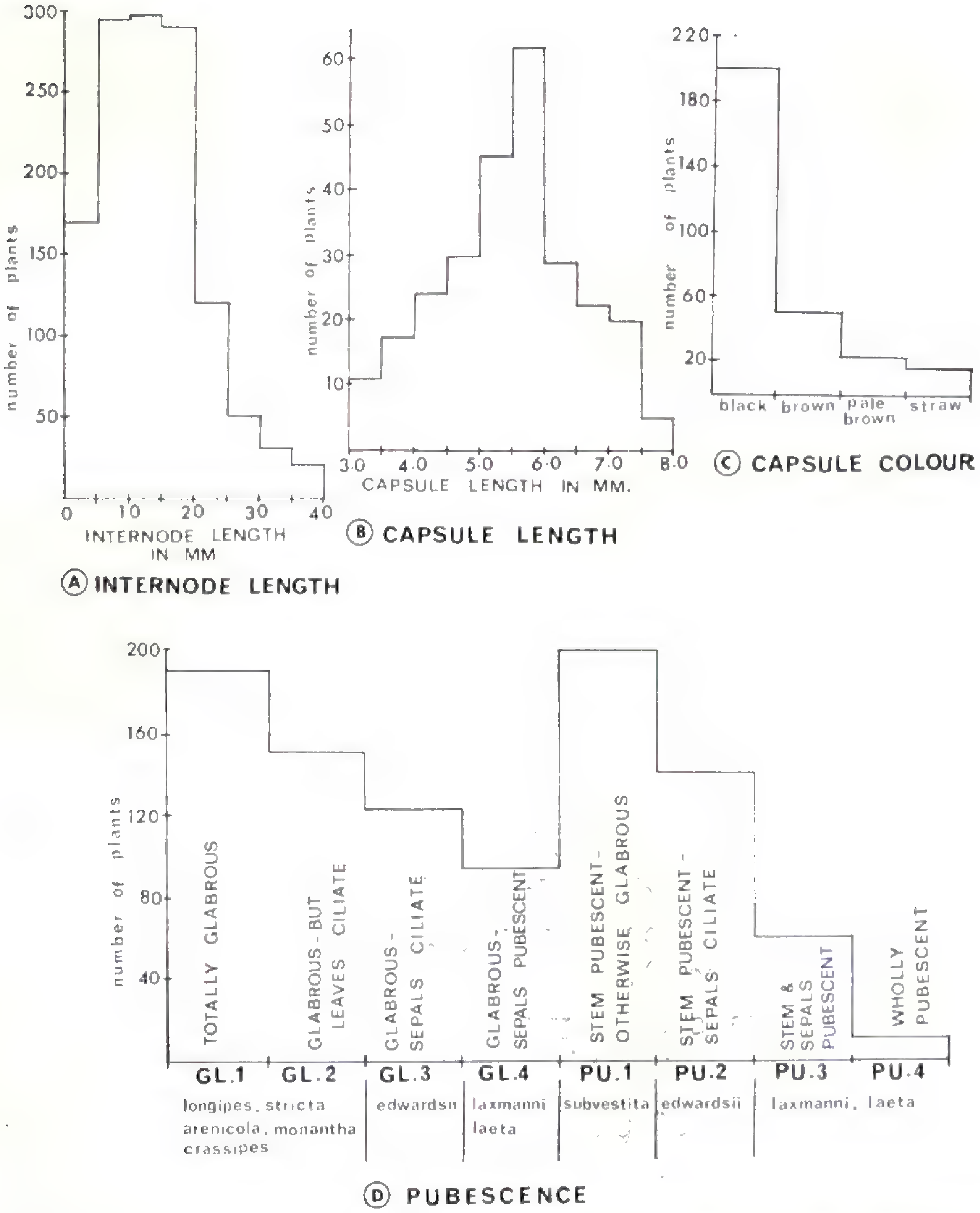

Figure 1. Histograms for measurable characters in the *Stellaria longipes* complex.

The characteristics of the mature capsule teeth (reflexed, spreading or erect) were also recorded. In the plants we studied 77.9% had erect teeth, 18.6% had spreading teeth and 3.5% had reflexed teeth.

Pubescence. This is the most variable character and the complexity in the pattern of pubescence has led to the description of several taxa by previous workers. The aerial parts of the plant vary considerably in respect of pubescence, and in some degree this variation tends to be independent in the different organs. Data were recorded on the following basis.

GL. 1 — totally glabrous (includes *S. longipes, S. stricta, S. arenicola, S. monantha, S. crassipes*).

GL. 2 — glabrous except for the leaves which are ciliate towards the base or on the margins (includes the same taxa as in GL. 1).

GL. 3 — stem and leaves glabrous, sepals ciliate on the margins (includes *S. Edwardsii*).

GL. 4 — stem and leaves glabrous, sepals pubescent on the outer surface (includes *S. Laxmanni* and *S. laeta*).

PU. 1 — stem and leaves pubescent, sepals and pedicels glabrous (includes *S. subvestita*).

PU. 2 — stem and leaves pubescent, sepals ciliate only on the margins, pedicels more or less glabrous (includes *S. Edwardsii*).

PU. 3 — stem and sepals pubescent, leaves and pedicels thinly pubescent (includes *S. Laxmanni* and *S. laeta*).

PU. 4 — plants densely pubescent throughout (includes *S. Laxmanni* and *S. laeta*).

The distribution of plants belonging to these pubescence types is shown in Fig. 1D.

Leaf. Leaves are usually green to dark green in colour, though glaucous ones are of common occurrence in most

populations. The usual leaf shape is lanceolate to linear-lanceolate. However, plants with oblong, ovate, or ovate-lanceolate leaves are not uncommon. Leaf length varies from 3 to 40 mm. and width from 0.5 to 5.0 mm. We decided not to undertake a detailed analysis of leaf measurements when it was observed that leaf proportions changed radically in our cultivated material during the course of development. As a result plants which had ovate leaves in their winter state, produced progressively longer and narrower ones during the flowering season, though the extent of this variation differed from population to population. In our cultivated material this sequence of leaf shape frequently remained intact in mature plants, though in material grown in the wild it is not usually apparent.

Other characters. Several other characters were examined but the data from them proved to be of little value and have been omitted from this account. These characters included the development of a scarious margin on the sepals, seed size and seed sculpturing.

DISCUSSION

Recent authors differ in their treatment of variation in the *Stellaria longipes* complex. Polunin (1959) regarded it as a single very variable species. Böcher (1951) and Hultén (1943) recognised 6 species, Porsild (1963) recognised 9, whilst Hultén (1968) in a subsequent revision, and Boivin (1966) accepted 4 species. All these workers based their taxonomy on the characters used in the present study, laying particular stress on pubescence, leaf shape and the development of the inflorescence and scarious bracts. Our own efforts to use the keys and descriptions of these workers have been only partially successful and many specimens appear to us to be undeterminable. Philipp (1972), in a recent study of material from Greenland, found that about half her specimens were intermediate between 2 or more of the species.

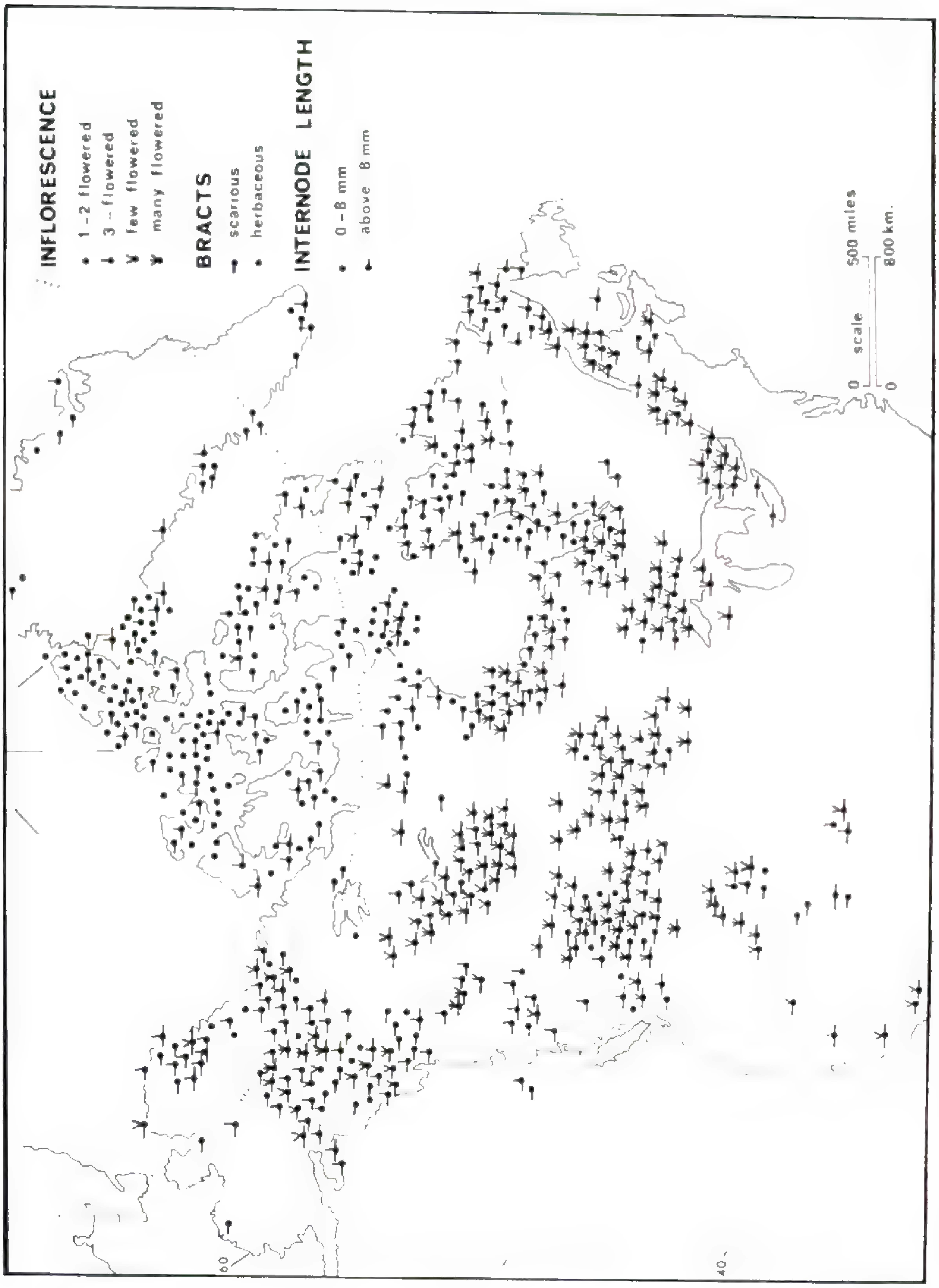

Figure 2. Map showing distribution and association of three characters — inflorescence, bracts and internode length — in *Stellaria longipes*.

For the recognition of taxa at the level of the subspecies and above, not only must there be visible morphological differences, but these differences must be associated, and not distributed at random through the individuals of the population. Furthermore there must be some basis for assuming that these characters are not just phenotypic responses to different environmental conditions. It is appropriate that we examine the pattern of variation in *Stellaria longipes* to determine to what extent the above criteria apply.

All the variation which we have studied in *Stellaria longipes* is of a quantitative nature and shows no discontinuities. This in itself makes the recognition of taxa within this complex of questionable value. The interfertility of the various cytotypes of the *S. longipes* complex has been demonstrated (Chinnappa and Morton, 1974). Hybridization between the cytotypes accounts for the wide range of chromosome numbers found in this complex, and undoubtedly contributes to the lack of discontinuity in morphological characters. Some degree of association of characters is apparent from our analysis of variation. In particular there is a clear tendency for the number of flowers in the inflorescence to be correlated with internode length and the occurrence of scarious bracts (Fig. 2). This correlation, however, has a north to south distribution suggestive either of clinal variation or of a phenotypic response to climate. Thus, low single-flowered plants, lacking scarious bracts, predominate in the arctic, and there is a progressive development in internode length, flower number and scarious bracts in plants towards the south, except in the mountains and other very exposed habitats.

Pubescence also shows a similar north to south trend (Fig. 3) with glabrous plants predominating in the south. However, the pattern of pubescence is complex and usually varies greatly amongst the individual plants of each population. Figure 4 shows this for a population at Churchill, Manitoba. Similar results were obtained from an analysis

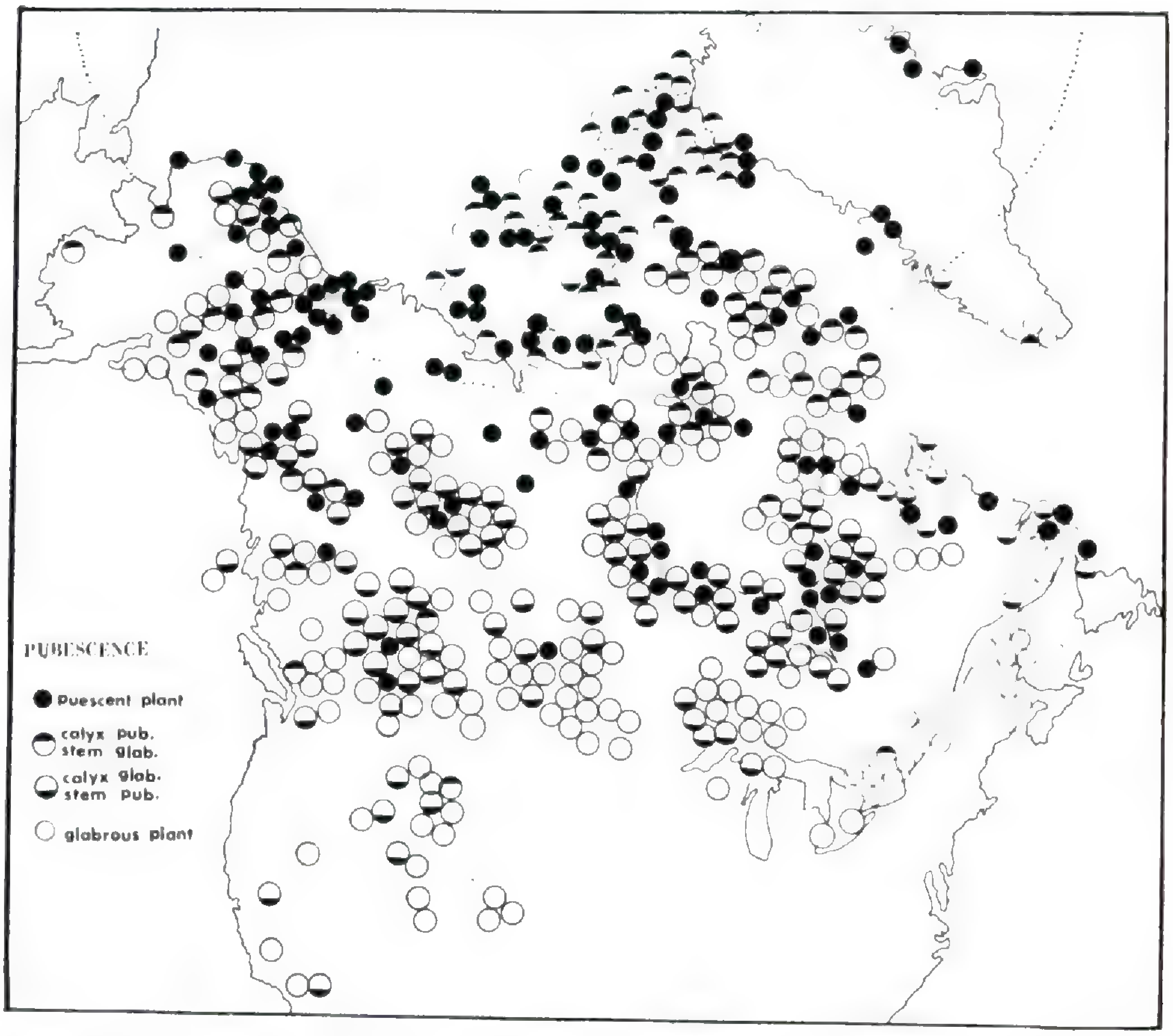

Figure 3. Map showing distribution of pubescence in *Stellaria longipes.*

of other populations. Only occasionally are populations homogeneous in pubescence pattern, and such populations are usually the smaller, more isolated ones. The north to south correlation which exists between pubescence and the characters used in Fig. 2 (bracts, inflorescence and internode) is at best only a broad geographical trend and there is considerable variation within most populations and in most regions. Hence, there is little basis here for the recognition of taxa. This is apparent in Fig. 5 where these characters, together with ones from the capsule, are combined in a single pictorial scatter diagram. It will be noted that the characters used in Fig. 5 include those regarded as being diagnostic for the various taxa included in this species complex.

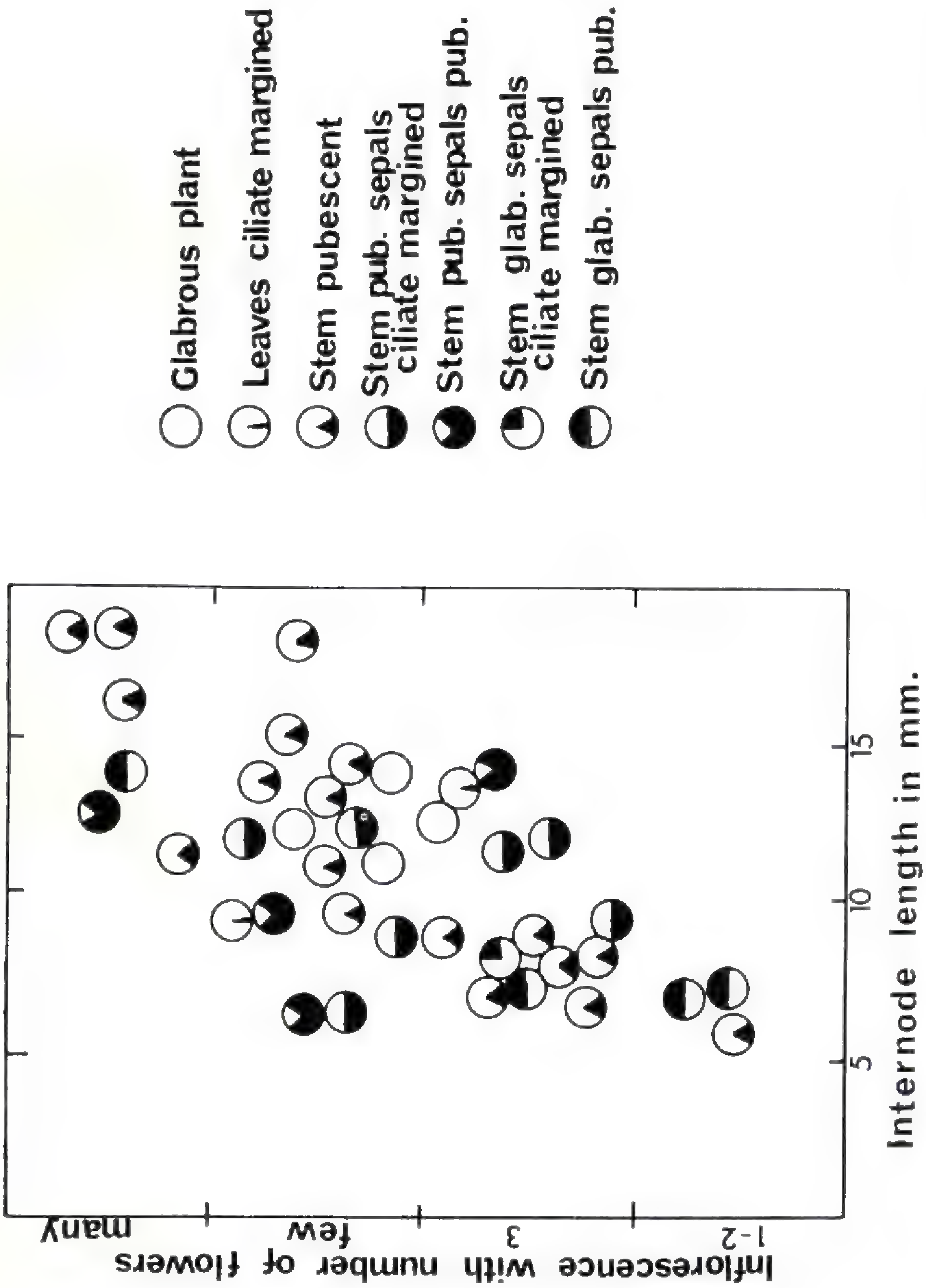

Figure 4. Variation in pubescence amongst a population of *Stellaria longipes* at Churchill, Manitoba. Each circle represents one plant.

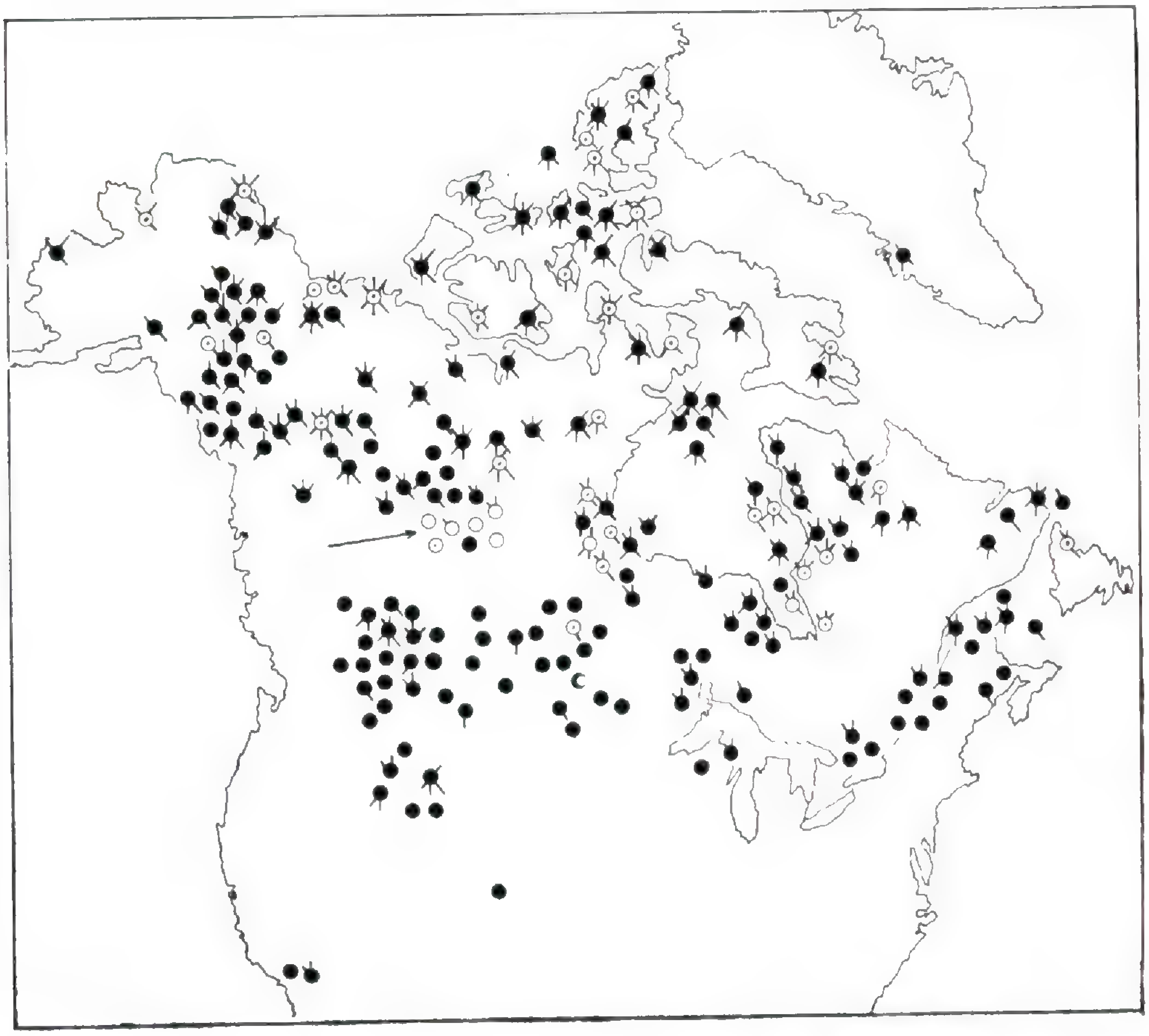

Figure 5. Map showing the distribution and association of capsule, inflorescence, pubescence, habit and internode characters in *Stellaria longipes*. For explanation of symbols see Fig. 6. The arrow indicates the approximate location of Lake Athabasca.

All populations, except those in the region of Lake Athabasca (see Fig. 5), have predominantly black (or dark brown) capsules with erect teeth. In the very specialized habitat of the shifting sand dunes on the south side of Lake Athabasca the situation is reversed, and plants with straw-coloured capsules and reflexed teeth predominate (Figs. 5 and 6). In this population, capsule characters (including a somewhat longer capsule) are associated with a characteristic habit of long, straggling stems with many-flowered inflorescences. Raup (1936) described these plants as *Stellaria arenicola*. However, these characters are not confined to plants from that locality, and

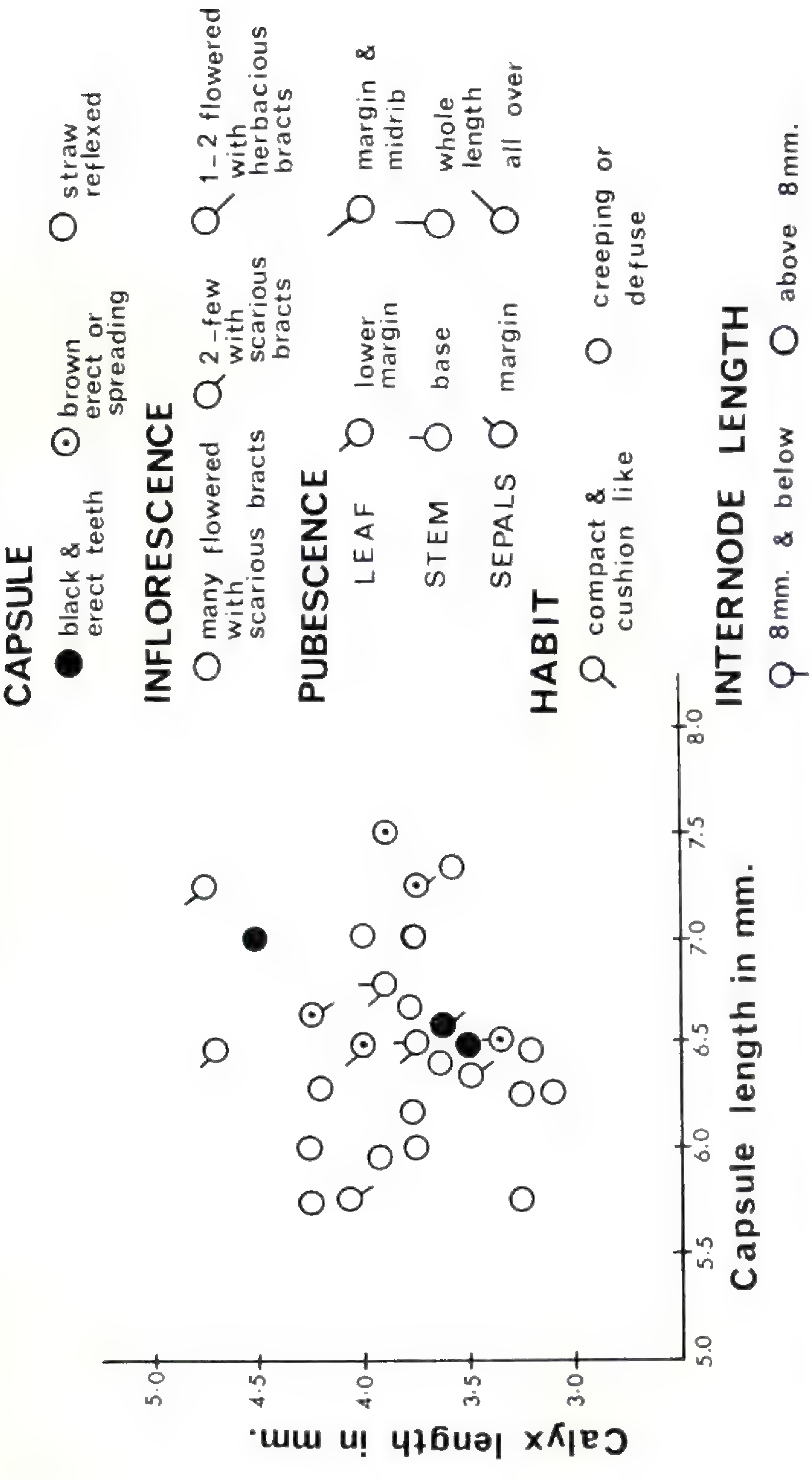

Figure 6. Variation in the Lake Athabasca population of *Stellaria longipes* (*S. arenicola* Raup).

they crop up at random in varying degrees of expression throughout the greater part of the range of the species (Fig. 5). Though paler capsule colour is usually associated with spreading to reflexed teeth, the combination of characters which make up *S. arenicola* (capsule size, colour, teeth, habit and inflorescence) has never been observed outside the Lake Athabasca population. But this population is not discrete and appears to introgress with other forms of *S. longipes* which grow in the vicinity (Fig. 6). Thus the status of *S. arenicola* as a species must be questioned, though some taxonomic recognition may be justified.

Hultén (1943), in describing *Stellaria crassipes*, characterized it as having pale-brown capsules with slightly reflexed teeth, whilst all other taxa were said to have dark brown to black capsules (Hultén did not recognize *S. arenicola*). However, Philipp (1972) observed that out of 42 samples of *S. longipes* s.l. from N.W. Greenland, which included *S. crassipes* Hult., all except one had dark brown capsules. Plants displaying all or some of the other characters, which Hultén associated with *S. crassipes* — short, fleshy, compact, glabrous stems, few-flowered inflorescences, ovate leaves and the near absence of a scarious margin to the bracts — are frequently encountered, particularly in the high arctic, but only rarely are all these characters associated in a single plant, together with pale capsule and slightly reflexed teeth, to produce the characteristic *S. crassipes* as described by Hultén. Hence, we can find little basis for maintaining a taxon, at any level, under the name *S. crassipes*.

It is apparent from this study that *Stellaria longipes* s.l. represents a continuum of variation within and between its many populations. Its characters occur in random combinations, some of which have been favoured with names by previous workers. There appears to us to be little justification for this except perhaps in the case of *S. arenicola* where a distinctive combination of characters persists in association with a very specialized habitat.

CONCLUSIONS

The principal results to emerge from this study are the following:

1. There is considerable variation in the taxonomic characters of *Stellaria longipes* in most of the populations throughout the greater part of the range of the species. This variation is not discrete and is of a quantitative or continuous nature, making the recognition of taxa difficult and of questionable value.

2. There is a clear north to south trend of variation in the following characters — internode length, pubescence, number of flowers in the inflorescence, and the occurrence of scarious bracts. Furthermore, variation in the last 3 characters is usually correlated, but this variation, along with that in leaf shape, is probably under considerable environmental and developmental influence and may not be genetically determined. Thus its taxonomic value is questionable.

3. The populations on the Lake Athabasca sand dunes, named *Stellaria arenicola* Raup, are distinctive and show a sufficiently marked correlation of characters to justify taxonomic recognition. Though these characters occur randomly throughout the range of the species in North America, only at Lake Athabasca are they associated in a high proportion of the individuals in the population. *Stellaria arenicola* appears to introgress freely with other forms of *S. longipes* which grow in the vicinity. Hence, the specific status of *S. arenicola* is questionable and it appears more appropriate to treat it at an infra-specific level within *S. longipes*.

4. A satisfactory understanding of variation in the *Stellaria longipes* complex must await an experimental study to determine its genetic basis and the reproductive biology of the component populations. Such a study has been undertaken and will be reported in a subsequent paper.

ACKNOWLEDGEMENTS

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REFERENCES

ANDERSON, J. P. 1959. Flora of Alaska and adjacent parts of Canada. The Iowa State Univ. Press. 543 pp.

ANDERSON, E. 1949. Introgressive hybridization. Hafner Pub. Co. N.Y. 109 pp.

BÖCHER, T. W. 1951. Studies on the distribution of the units within the collective species of *Stellaria longipes*. Bot. Tidsskr. **48**: 402-420.

BOIVIN, B. 1966. Enumeration des plantes du Canada. Naturaliste Can. **93**: 371-437.

CHINNAPPA, C. C. 1973. A biosystematic study of the *Stellaria longipes* complex (Caryophyllaceae) Ph.D. Thesis. Univ. of Waterloo.

————, & J. K. MORTON. 1974. The cytology of *Stellaria longipes* Goldie and the evolution of chromosome number. Can. J. Genet. Cytol. **16**: 499-514.

HULTÉN, E. 1943. *Stellaria longipes* Goldie and its allies. Bot. Notiser **1943**: 251-270.

————. 1968. Flora of Alaska and neighboring territories. Stanford Univ. Press. Calif. 1008 pp.

PHILIPP, M. 1972. The *Stellaria longipes* group in N.W. Greenland. Cytological and morphological investigations. Bot. Tidsskr. **67**: 64-75.

POLUNIN, N. 1959. Circumpolar arctic flora. Oxford. 514 pp.

PORSILD, A. E. 1963. *Stellaria longipes* Goldie and its allies in North America. Nat. Mus. Canada Bull. **186**: 1-35.

RAUP, H. M. 1936. Phytogeographic studies in the Athabasca-Great Slave Lake region. I. Catalogue of vascular plants. J. Arn. Arb. **17**: 248-249.

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NOMENCLATURE, TAXONOMY, AND BIOSYSTEMATICS OF VACCINIUM SECTION CYANOCOCCUS (THE BLUEBERRIES) IN NORTH AMERICA. I. NATURAL BARRIERS TO GENE EXCHANGE BETWEEN VACCINIUM ANGUSTIFOLIUM AIT. AND VACCINIUM CORYMBOSUM L.

S. P. Vander Kloet

A number of clustering strategies such as flexible sorting (Lance and Williams, 1967), average link (Upgma), and Burr's (1970) incremental sum of squares (McNeill in preparation) and other techniques such as Rubin's (1967) clustering strategy (see Vander Kloet, 1972) were used on various subsets of 670 blueberry colonies collected along the Frontenac axis in Ontario and adjacent New York in 1970. Two morphologically distinct groups (*inter alia*) are consistently formed. One of these groups may be referred to the taxon *Vaccinium angustifolium* Aiton (sensu Hall and Aalders, 1961, and D. W. Smith, 1969, non Camp, 1945) and the other to *Vaccinium corymbosum sensu lato.*

Both of these taxa are tetraploid (Longley, 1927, Newcomer, 1941, Hall and Aalders, 1961, Löve and Löve, 1966). Darrow *et al.* (1944) reported that *Vaccinium angustifolium* was diploid; however, the supporting specimen they cite cannot be located. Since no cytological barriers to interbreeding exist between tetraploids, these taxa are considered compatible (Camp, 1942, 1945). They are sympatric in the sense that all the northern populations of *V. corymbosum* fall completely within the range of *V. angustifolium.* Furthermore, both species are acidophilic, although habitat preferences do exist. *Vaccinium corymbosum* occurs in a variety of wet habitats such as bogs, swamps, wet depressions, seepage slopes and ditch, river, and lake margins, while *V. angustifolium* occurs not only on a variety of dry sites such as granite outcrops, sand hills, headlands,

Table 1: Differences between *V. angustifolium* and *V. corymbosum* which may result in ethological isolation.

Taxon	habitat	plant height in cm	corolla length in mm	1971 mean blooming date
V. angustifolium	granite outcrops quartzite outcrops sandstone pavements oak parklands	10–60	4–6	May 18 ± 3 days
V. corymbosum	bogs swamps wet depressions	100–300	6–11	May 30 ± 4 days

poverty grass meadows and oak parklands, but also in raised bogs, along lake margins and along ditch banks where it occurs with *V. corymbosum.*

Along the Frontenac axis *Vaccinium corymbosum* occurs in bogs, swamps, occasionally in wet depressions on granite and quartzite outcrops while *V. angustifolium* occurs on sandstone pavements, oak parklands and on granite and quartzite outcrops where it comes into contact with *V. corymbosum.* Even here the taxa maintain their morphological distinctness although two, or at most three, hybrids were found in all localities where both species occur together.

It is against this background that the present investigation of the pollination syndrome (*sensu* Levin, 1971) of these two species was undertaken; Table 1 contrasts the characteristics which may lead to discrimination by the pollinator fauna and thus result in ethological isolation. Accordingly, in 1971, following a procedure described by Judd (1966), I collected pollinators on plants of these species. Pollinators were identified by M. Ivanochko (Vespidae), B. V. Peterson and G. E. Shewell (Diptera) and H. E. Milliron (other Hymenoptera) of the Entomology Research Institute, Canada Department of Agriculture, Ottawa, Ontario. Table 2 lists the common bee species collected and their frequency of occurrence. It suggests that, in fact, the two species utilize different segments of the pollinator fauna. No honey bees and very few andrenids were caught on *V. corymbosum;* however, both taxa shared several of the *Bombus spp.* especially *Bombus bimaculatus.*

This overlap in pollinator taxa might not involve opportunities for pollen transfer if there were high pollinator specificity. Pollinator specificity was first reported by Aristotle, corroborated by Darwin (see Grant, 1950) and is still believed to be important (Heinrich, 1973). This concept is based on strict observation of preference for a single floral signal, i.e., the *Bombus ternarius* which I followed for 83 consecutive visits chose only *Vaccinium angustifolium* corollas.

Table 2: Numerical estimate of pollinators collected on *Vaccinium angustifolium* from four localities and on *Vaccinium corymbosum* from one locality.

Pollinators	Number caught on *V. angustifolium*	Number caught on *V. corymbosum*
Bombus bimaculatus*	49 (12)	20
B. terricola	30 (8)	3
B. ternarius	17 (4)	3
B. impatiens	12 (3)	2
B. perplexus	9 (2)	20
B. affinis	13 (3)	—
B. griseocollis	2 (+)	6
B. pensylvanicum	2 (+)	2
B. fervidus	1 (+)	—
B. vagans	1 (+)	10
B. sandersoni	1 (+)	2
Psithyrus ashtoni	1 (+)	4
Apis mellifera	41 (10)	—
Andrena carlini	130 (38)	1
A. vicina	78 (19)	2
A. crataegi	6 (2)	1
A. mandibus	—	1
Nomada spp.	14 (3)	—
Osmia atriventris	—	3
Evylacus truncatus	—	3
Augochlora pura	—	6

*() brackets indicate the average number of pollinators per locality.

The extent of flower constancy of bees can be verified by examination of the corbicular pollen loads. This is a time consuming procedure whose results are sometimes difficult to interpret. Grant (1950) has reviewed several pollen pellet analyses: those of Betts (1920), Brittain & Newton (1933), and Clements and Long (1923). Each of these workers reported that bees carried mixed pollen loads. However, Grant (1950, p. 384) reexamined some of Clements and Long's data and concluded that a 95% pure load in *Apis mellifera* is tantamount to a pure load. In effect Grant has belittled these reports.

In spite of these findings, the concept of ethological isolation remains entrenched in the literature and is frequently cited as part of the argument in favour of biological separation of taxa through floral signal isolation as in Levin (1971).

Since observation partially demonstrated ethological isolation between *Vaccinium angustifolium* and *V. corymbosum* colonies along the Frontenac axis, an examination was made of pollen pellets from a random sample of pollinators.

MATERIALS AND METHODS

From May 15, 1972, to June 10, 1972, five sampling areas were visited weekly, viz., (1) Rock Dunder, a 2 hm^2 granite outcrop near Morton, Ont. (031/309, 31 ^{c}/9 E). *Vaccinium angustifolium* colonies are abundant on this outcrop. (2) Burnt Hill, a 1.2 hm^2 granite outcrop near Morton, Ont. (035/297, 31 ^{c}/9 E). *Vaccinium angustifolium* colonies are abundant on this outcrop; moreover, in a small permanently wet depression a small population of *V. corymbosum* occurs. (3) Mt. Fitzsimmons, a steep granite outcrop near Lansdowne, Ont. (172/134, 31 ^{c}/8 E), supports a large population of *V. angustifolium* and along the margin of a *Nemopanthus mucronata* shrub carr (which occupies the centre of a small, permanently wet depression on top of the mountain) are several large colonies of *V. corymbosum*. (4) The Kaladar Jack Pine Ridge, a massive granite-gneiss ridge 0.5 km north of Kaladar, Ont. (312/475, 31

^{c}/11 E) on which *V. angustifolium* occurs in abundance. (5) The Hebert Bog, near Upper Rock Lake, Frontenac County, Ont. (875/280, 31 ^{c}/8 W), a 2 hm^2 spruce bog which contains several large colonies of *V. corymbosum*, but no *V. angustifolium*. However, the surrounding granite-gneiss outcrops have several colonies of *V. angustifolium*.

At each of these sites, six colonies were chosen at random and every pollinator, which visited the colony in a ten minute period and hit at least three consecutive corollas, was trapped in a cyanide bottle, transferred to a vial of 70% alcohol, labelled, and stored in the refrigerator. In addition, flowers from all taxa in bloom at each sampling time were collected and, using the Wodehouse (1935) technique, reference pollen slides were prepared.

The vial containing the pollinator in 70% alcohol was shaken in order to transfer the pollen grains from the insect body into the alcohol, which was then decanted and centrifuged; after the supernatant was poured off, four drops of glycerol were added to the pollen pellet, mixed, and a single drop put on a slide, covered and sealed with a clear fingernail polish.

The slide was scanned under high power and the first 50 grains identified and recorded, using in the first instance the prepared reference slides and secondly the pollen atlases of Richard (1970) and of Kapp (1969).

RESULTS

Of the 50 pollen loads examined, only one was pure; i.e., the pollen load was composed entirely of pollen grains which could be assigned to *Vaccinium angustifolium*. The remaining 49 were mixed. However, if the investigator's error, the presence of wind borne pollen on the collecting sites, and accidental straying by the pollinator are taken into account, a cumulative background contamination of 10% or even 20% could occur. Even with such a liberal allowance for error, only 22% of the loads examined could be assigned to the "pure" class.

Table 3: Pollen load analysis of pollinators visiting *Vaccinium angustifolium* and *V. corymbosum* along the Frontenac axis.

pollen load	low <100 grains	moderate 100-10,000 grains	high >10,000 grains
pure loads >80%	1	2	8
mixed loads 2 spp.	4	5	6
mixed loads 3 spp.	7	3	—
mixed loads 4 spp.	14	—	—

Table 3 gives these results in terms of "pure" and mixed classes only, since no difference in the ratio of pure to mixed could be detected in either loads examined from bees collected on corollas of *Vaccinium angustifolium* or *V. corymbosum* or in loads examined from different genera of bees. Out of the loads from four *Apis mellifera* examined one carried a pure load; out of the 19 loads from *Andrena spp.* six carried pure loads; out of the 16 loads from *Bombus spp.* four carried pure loads. No difference in constancy could be detected between sites.

CONCLUSION

This random collection of pollinators had few that were constant to a single floral signal. Linsley *et al.* (1963, 1964) have argued that pollinator specificity is a plastic response subject to modification by immediate circumstances. It is most pronounced in areas of high food-plant density. At low food-plant density, a pollinator is apt to feed on any suitable plant. This latter condition seems to fit the Frontenac axis condition quite well. Many of the plant species on these outcrops break dormancy during

the last week of April and begin to bloom in the mid-May period, for example, *Arctostaphylos uva-ursi* L., *Fragaria virginiana* Duchesne, *Amelanchier sanguinea* Pursh (DC.), *Amelanchier spicata* (Lam.) K. Koch., *Amelanchier arborea* (Michx. f.) Fern., *Prunus pensylvanica* L. f., *Prunus virginiana* L., *Aronia melanocarpa* (Michx.) Britton, and *Comandra umbellata* (L.) Nutt. Also, hibernating queen bees emerge at this time; these queens may try a number of different floral signals before they begin to specialize. Twenty-seven bees (or 58%) of the random sample had fewer than 100 pollen grains on their entire body.

The analysis of the loads suggests that ethological isolation between *Vaccinium angustifolium* and *V. corymbosum* does not exist along the Frontenac axis. Although this evidence is fairly conclusive for this area it would be unreasonable to generalize from such a local sampling regime. A valid generalization would have to be based on a wider sampling of the entire range of the species. Hence, using the same collecting technique as described above, pollinators were collected from several populations of *V. angustifolium* and *V. corymbosum* in Nova Scotia. Additional pollinators were also collected from several other *Vaccinium* section *Cyanococcus* species, when they occurred with either *V. angustifolium* or *V. corymbosum* in both Nova Scotia and Florida, in order to assess the level of constancy between *V. angustifolium* or *V. corymbosum* and their sister groups.

Description of additional sampling sites (methodology is the same as above): (1) From February 28 to March 3, 1973, 13 pollinators were collected on corollas of *Vaccinium myrsinites* and *V. corymbosum* which occur along margins of and in fire trenches cut through pine flatwoods, and on the fringes of Lake Annie near Archbold Biological Field Station in Highlands County, Florida. (2) From May 27 to June 15, 1973, 87 pollinators were collected on five sites throughout Nova Scotia: a shrub zone, which contained both *V. corymbosum* and *V. angustifolium* colonies, surrounding Lake George, near Port Maitland, Yarmouth County; sand hills with *V. myrtilloides* and *V. angusti-*

folium on the northern edge of Wolfville, Kings County; a blueberry (*V. angustifolium*) headland near High Head, Yarmouth County; an abandoned pasture, which has been invaded by *V. angustifolium* and *V. myrtilloides*, 1.5 km N of West Branch, Pictou County; and finally an extensive blueberry barren (*V. angustifolium*) 2.6 km W of Merland, Antigonish County.

Results: The results, given in table 4, show the same pattern as those given in table 3. Again the incidence of low pollen loads is associated with mixed pollen loads, and vice versa, a high pollen load with a tendency towards specificity.

Table 4: Pollen load analysis of pollinators visiting *Vaccinium* § *Cyanococcus* in Florida and Nova Scotia heath communities.

pollen load	low <100 grains	moderate 100–10,000 grains	high >10,000 grains
pure loads >80%	5	9	12
mixed loads 2 spp	14	10	9
mixed loads 3 spp	13	2	5
mixed loads 4 spp	16	4	1

Moreover, these data do not support any more readily than the previous data the concept of ethological isolation in *Vaccinium* section *Cyanococcus*. Indeed the opposite seems to be more valid; pollinator activity increases the probability of gene exchange between taxa. The differences between taxa, such as those given in Table 1, are probably the result of selection pressures of the habitat.

In 1970, a series of warm nights, which began on April 22 and continued until May 5, resulted in rapid floral axis

expansion in *Vaccinium corymbosum* colonies in bogs and depressions (indeed several precocious colonies of *V. angustifolium* on the surrounding upland outcrops had already begun to bloom). However, on the nights of May 5 and 6, the temperature fell to −3°C and −2°C respectively in the hollows, while on the slopes and uplands the temperature remained at 0°C and 1°C respectively, causing severe frost damage to the expanded flower buds of *V. corymbosum* while the *V. angustifolium* flowers were not damaged at all.

On August 21, 1970, only the serotinous colonies of *Vaccinium corymbosum* bore fruit; the frost damaged shrubs had a few green berries which had been infected by *Molinia spp.* and contained no ripe ovules.

Brown, McKay and Chapman (1968) give May 15 as the mean date for the last occurrence of 0°C for the sample area. But since the topography is heterogeneous, the probability of frost occurring at a later date in the hollows is very high (Geiger, 1966, p. 393).

Vaccinium growth and development is closely related to night-time temperatures (Geiger, 1966, p. 439). But if night-time temperatures fall below −2.2°C for more than two consecutive hours irreversible frost damage occurs (Hall, Aalders and Newbery, 1971). In short, along the Frontenac axis, selection is against precocious shrubs of *V. corymbosum.*

The reverse holds for *Vaccinium angustifolium;* here selection acts against serotinous colonies. The soil on the granite and quartzite ridges and outcrops is very shallow and discontinuous, which, in conjunction with 40-45°C temperatures at ground level during June, July and August, and unpredictable precipitation, often result in severe summer droughts (Vander Kloet, 1973). Consequently, late flowering colonies of *V. angustifolium* produce few if any mature berries. I have observed racemes of wilted green berries and fully formed leaf abscission layers on July 1, 1970 and 1973. In those years only the colonies that flowered between May 5 and May 12 fruited abundantly.

It is these countervailing selective pressures which account for the phenological difference given in Table 1. Moreover, since the pollinator data suggest some constancy and some specialization in feeding behaviour, the different flower size and plant height may well restrict some cross-pollination between the species. It is not a single factor but rather a combination of all these factors — habitat, phenology, plant height, corolla length, and pollinator frequency and constancy — which is effective in the evolution and the retention of the species' distinctiveness.

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LITERATURE CITED

BETTS, A. D. 1920. The constancy of the pollen-collecting bee. Bee World 2: 10-11.

BRITTAIN, W. H., & D. E. NEWTON. 1933. A study in the relative constancy of hive bees in pollen gathering. Can. J. Res.: 334-349.

BROWN, D. M., G. A. MCKAY, & L. J. CHAPMAN. 1968. The climate of southern Ontario. Climatological studies; 5, Meteorological Br., Canada Department of Transport. Queen's Printer, Ottawa.

BURR, E. J. 1970. Cluster sorting with mixed character types. II. Fusion strategies. Aust. Comp. J. 2: 98-102.

CAMP, W. H. 1942. On the structure of populations in the genus *Vaccinium*. Brittonia 4: 189-204.

————. 1945. The North American blueberries with notes on other groups of Vacciniaceae. Brittonia 5: 203-275.

CLEMENTS, F. E. & F. L. LONG. 1923. Experimental pollination. An outline of the ecology of flowers and insects. Publ. Carnegie Inst. Wash., 336.

DARROW, G. M., W. H. CAMP, H. E. FISCHER, & H. DERMEN. 1944. Chromosome numbers in *Vaccinium* and related groups. Bull. Torrey Bot. Club 17: 498-506.

GEIGER, R. 1966. The climate near the ground. Harvard Univ. Pr., Cambridge, Mass.

Grant, V. 1950. The flower constancy of bees. Bot. Rev. **16**: 397-398.

Hall, I. V., & L. E. Aalders. 1961. Cytotaxonomy of lowbush blueberries in eastern Canada. Amer. J. Bot. **48**: 199-201.

————, & R. J. Newbery. 1971. Frost injury to flowers and developing fruits of the lowbush blueberry as measured by impairment of fruit set. Naturaliste Can. **98**: 1053-1057.

Heinrich, B. 1973. The energetics of the bumblebee. Sci. Am. **228**: 96-102.

Judd, W. W. 1966. Studies of the Byron Bog in southwestern Ontario. XXVII. Insects associated with flowering blueberry, *Vaccinium atrococcum* (Gray) Heller. Can. Field. Nat. **80**: 242-244.

Kapp, R. O. 1969. How to know pollen and spores. Wm. C. Brown, Co., Dubuque, Iowa.

Lance, G. N., & W. T. Williams. 1967. A general theory of classificatory sorting strategies. I. Hierarchical systems. Comp. J. **9**: 373-380.

Levin, D. A. 1971. The origin of reproductive isolating mechanisms in flowering plants. Taxon **20**: 91-113.

Linsley, E. G., J. W. MacSwain, & P. H. Raven. 1963. Comparative behavior of bees and Onagraceae. I. *Oenothera* bees of the Colorado desert. II. *Oenothera* bees of the Great Basin. Univ. Calif. Publ. Entomol. **33**: 1-58.

————. 1964. Comparative behavior of bees and Onagraceae. III. *Oenothera* bees of the Mohave desert, California. Univ. Calif. Publ. Entomol. **33**: 59-98.

Longley, A. E. 1927. Chromosomes in *Vaccinium*. Science **66**: 566-568.

Löve, A., & D. Löve. 1966. Cytotaxonomy of the alpine vascular plants of Mount Washington. Univ. of Colorado Studies Ser. Biol. **24**: 1-74.

Newcomer, E. H. 1941. Chromosome numbers of some species and varieties of *Vaccinium* and related genera. Am. Soc. Hort. Sci. **38**: 468-470.

Richard, P. 1970. Atlas pollinique des arbres et de quelques arbustes indigènes du Québec. Naturaliste Can. **97**: 1-34, 97-161, 241-306.

Rubin, J. 1967. Optimal classification into groups: An approach for solving the taxonomy problem. J. Theoret. Biol. **15**: 103-144.

Smith, D. W. 1969. A taximetric study of *Vaccinium* in northeastern Ontario. Can. J. Bot. **47**: 1747-1759.

Vander Kloet, S. P. 1972. The North American blueberries revisited: a taxonomic study of *Vaccinium* section *Cyanococcus* Gray. Thesis, Queen's University at Kingston, Ont.

———. 1973. The biological status of pitch pine, *Pinus rigida* Miller, in Ontario and adjacent New York. Can. Field Nat. **87**: 249-253.

WODEHOUSE, R. P. 1935. Pollen grains. McGraw-Hill, New York.

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INVESTIGATIONS OF THE MARINE ALGAE OF SOUTH CAROLINA I. NEW RECORDS OF RHODOPHYTA

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The most extensive accounts of benthic marine algae occurring in South Carolina were included in larger surveys of marine algae from North America by William H. Harvey (1852, 1853, 1858), and from Beaufort, North Carolina and adjacent regions by W. D. Hoyt (1920). Their findings were based on brief visits to this state. Considering the dearth of information on the marine algae of the South Carolina coast, a preliminary survey of one of the major groups, the Rhodophyta, has been initiated. This paper newly records 31 taxa of red algae from this region.

MATERIALS AND METHODS

The intertidal collections (Fig. 1, Collection Stations 1-8) were made and identified by the first coauthor over the past several years. The pelagic collections (Fig. 1, Collection Stations 9-18) were obtained by dredging by Dr. R. B. Searles of Duke University from the R/V *Eastward,* Cruise E-7-74, June 11-12, 1974. The second coauthor participated in this cruise and identified the specimens. Representative specimens have been deposited in the Duke University Algal Herbarium.

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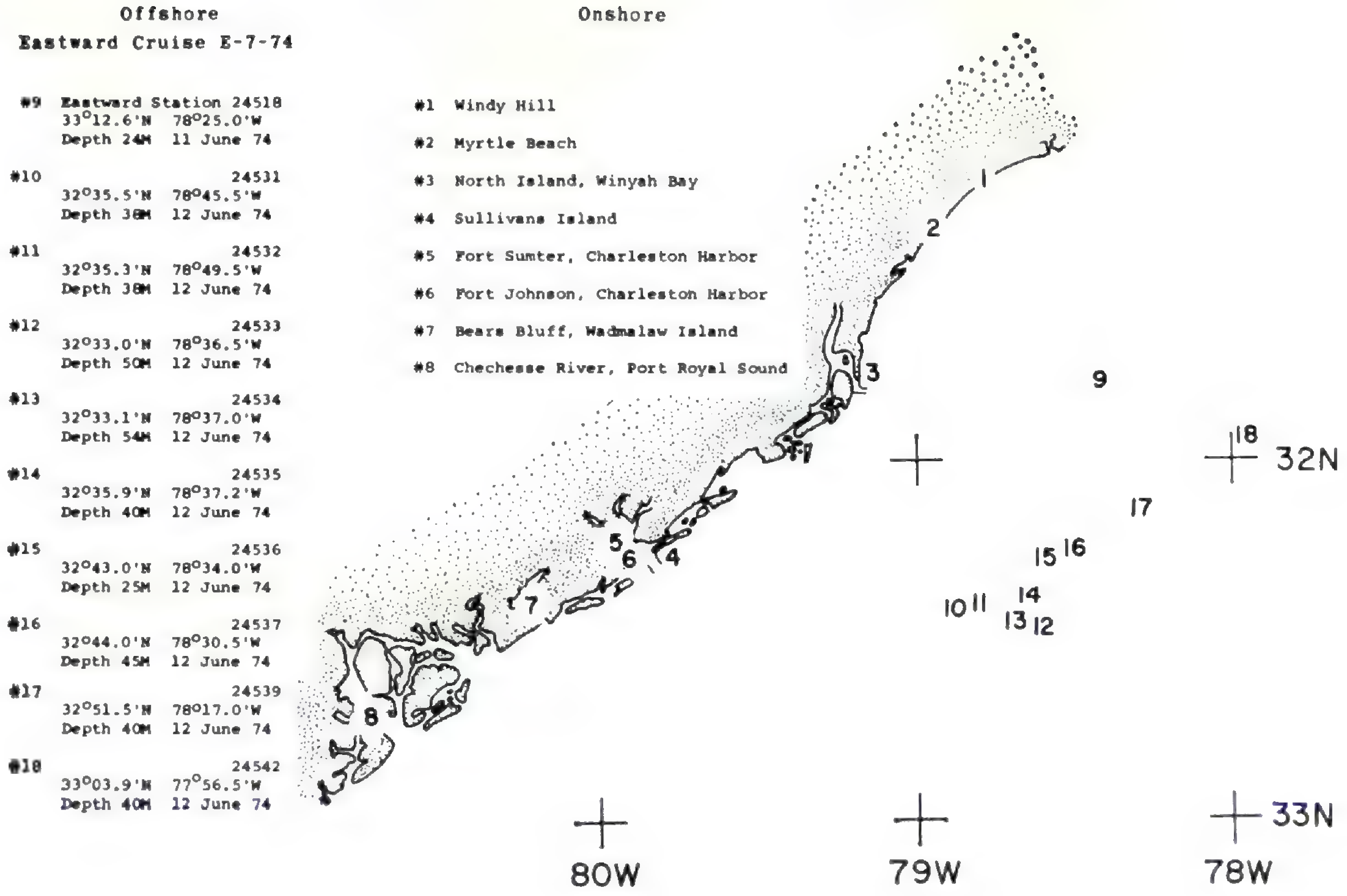

Figure 1. South Carolina collection stations.

HISTORICAL SUMMARY

Jacob W. Bailey (1848) published the first records of marine algae from South Carolina based on specimens sent to him by Professor Lewis R. Gibbes of Charleston. Bailey was assisted in the determinations by William H. Harvey of Trinity College, Dublin. This paper and one published the previous year by Bailey were the first phycological papers published in the United States (Zaneveld, 1966). Seven species were listed from South Carolina, but *Ectocarpus viridis* Harvey (= *E. siliculosus* (Dillwyn) Lyngbye) was inadvertently placed by Bailey in both the "Chlorospermeae" and the "Melanospermeae", thus reducing the species recorded from the state to 6 with three of the six in the "Rhodospermeae". Bailey later (1851), in an extensive report on desmids and diatoms from the southeastern United States, included 4 species of macroscopic marine algae. Three of the 4 species were red algae with 2 of these new rhodophycean records for South Carolina.

William H. Harvey stopped briefly at Charleston in January and March, 1850, in transit to and from Key West, Florida. Aided by L. R. Gibbes and H. W. Ravenal, he collected 29 species of marine algae from the Charleston area. Harvey included these findings in his monumental *Nereis Boreali-Americana* (1852-1858). Thirteen of the 17 red algae reported by Harvey (1853) were new records for the state. Harvey cited all of the species previously reported by Bailey with the exception of *Rhodymenia palmata* (L.) Greville, which was listed by Bailey in the 1848 paper. The latter species has not been recollected from South Carolina, and more than likely the plants identified as *R. palmata* are really *R. pseudopalmata* (Lamouroux) Silva, a species commonly found on the harbor jetties at Charleston.

Jordan (1874) and Farlow (1876) listed species of marine algae from South Carolina in distributional notes, but all of these records were taken from Harvey's *Nereis Boreali-Americana.*

Melvill spent the winter of 1871 and the spring and summer of the following year at Charleston. He reported (1875) 22 taxa of marine algae from this region, all but two of which had previously been cited by Bailey and Harvey. The two new additions, the pelagic brown alga, *Sargassum bacciferum* (Turner) C. Agardh (= *S. fluitans* Børgesen or *S. natans* (L.) Meyen), and a red alga, *Callithamnion baileyi* Harvey, were cited by Harvey in *Nereis Boreali-Americana* but were not reported from South Carolina.

Hoyt visited Georgetown, Pawleys Island, Charleston, and Port Royal Sound in South Carolina during the summer months of 1909. He commented (1920) on 21 species and a variety of marine algae from the state. The variety and 15 species were red algae, six of which represented new records for the state.

In April 1947, Stephenson and Stephenson (1952) studied intertidal zonation on the jetties, breakwaters, and seawalls in Charleston Harbor, the area around Bears Bluff Laboratory on Wadmalaw Island, and a narrow channel (Eliot Cut) connecting the Stono and Ashley Rivers. They reported 14 genera of algae with two of the genera not determined to species. Seven of the 12 genera determined to species were red algae. Three of the 7 reds were new records for the state, while the other 4 species probably represent taxa previously reported under different specific epithets.

During the years 1947 to 1949, Pearse and Williams (1951) investigated the biota of the submerged "black rock" formations off the coasts of North and South Carolina. On August 16-17, 1949, they made collections at a formation near Little River, South Carolina. Williams compiled the section of algal vegetation and listed 104 taxa from both states with 67 of these placed in the Rhodophyta. With the exception of the 'Carolinas only' notation under which he listed 11 taxa, the format used in the distributional synopsis has made it impossible to ascertain with certainty records for South Carolina. Five of the 11 taxa

cited under 'Carolinas only' represent new rhodophycean records for the state.

W. R. Taylor (1957, 1960) cited 41 species and 3 varieties of marine algae from South Carolina with 30 of these in the Rhodophyta. Most of the taxa listed by Taylor were previously reported by either Bailey, Harvey, Melvill or Hoyt.

Schneider (1975) reported two new and interesting additions to the South Carolina marine algal flora, *Acrosorium uncinatum* (Turner) Kylin and *Rhododictyon bermudensis* Taylor. The former species was collected by dredging at Collection Stations #13, 14, 16, 17 (Fig. 1), and the latter species at Station #13. Schneider and Searles (1976) have also collected five additional new taxa by dredging in the same region, including: *Hypnea volubilis* Searles, *Petroglossum undulatum* Schneider, *Sarcodiotheca divaricata* Taylor, *Rhodymenia divaricata* Dawson, and *Lithothamnium occidentale* (Foslie) Foslie. These 7 new offshore records, as well as the ones reported in this paper, attest to the richness and diversity of the deep water flora of this coast, and future exploration should yield many new additions.

Taxa of red algae previously reported from South Carolina are listed below. Some of these have been regarded as uncertain records for the state and are in need of reconfirmation.

Bangiales

Porphyra leucosticta Thuret in Jolis
Porphyra umbilicalis (L.) J. Agardh

Gelidiales

Gelidium corneum (Hudson) Lamouroux
Gelidium crinale (Turner) J. Agardh

Cryptonemiales

Grateloupia filicina (Wulfen) C. Agardh
Grateloupia gibbesii Harvey

Gigartinales

Gracilaria foliifera (Forsskål) Børgesen
Gracilaria foliifera var. *angustissima* (C. Agardh) Taylor
Gracilaria sjoestedtii Kylin
Gracilaria verrucosa (Hudson) Papenfuss
Eucheuma gelidium J. Agardh
Neoagardhiella baileyi (Harvey *ex* Kützing) Wynne & Taylor
Soliera tenera (J. Agardh) Wynne & Taylor
Hypnea musciformis (Wulfen) Lamouroux

Rhodymeniales

Rhodymenia pseudopalmata (Lamoroux) Silva
Rhodymenia pseudopalmata var. *caroliniana* Taylor
Lomentaria baileyana (Harvey) Farlow

Ceramiales

Callithamnion byssoideum Arnott *ex* Harvey in Hooker
Callithamnion polyspermum C. Agardh
Ceramium rubrum (Hudson) J. Agardh
Ceramium strictum (Kützing) Harvey
Pleonosporium borreri (J. E. Smith) Nägeli *ex* Harvey
Caloglossa leprieurii (Montagne) J. Agardh
Grinnellia americana (C. Agardh) Harvey
Calonitophyllum medium (Hoyt) Aregood
Hypoglossum tenuifolium (Harvey) J. Agardh
Dasya baillouviana (Gmelin) Montagne
Bostrychia radicans (Montagne) Montagne
Bostrychia radicans form *moniliforme* Post
Chondria atropurpurea Harvey
Herposiphonia tenella (C. Agardh) Schmitz form *secunda* (C. Agardh) Hollenberg
Polysiphonia denudata (Dillwyn) Kützing
Polysiphonia harveyi Baileyi
Polysiphonia nigrescens (Hudson) Greville
Spyridia filamentosa (Wulfen) Harvey

RESULTS

List of new records of red algae from South Carolina with Collection Stations.

Bangiales

- *Bangia atropurpurea* (Roth) C. Agardh — 4, 5

Gelidiales

- *Gelidium pusillum* (Stackhouse) Le Jolis — 6, 7

Cryptonemiales

- *Corallina officinalis* L. — 2
- *Halymenia hancocki* Taylor — 10, 11, 17, 18
- *Heteroderma lejolisii* (Rosanoff) Foslie — 2
- *Peyssonnelia rubra* (Greville) J. Agardh — 12, 13, 14, 16, 17

Gigartinales

- *Gymnogongrus griffithsiae* (Turner) Martius — 2, 3
- *Gracilaria mammillaris* (Montagne) Howe — 9, 12, 13, 14, 16, 17, 18
- *Plocamium brasiliense* (Greville) Howe & Taylor — 12, 14, 16, 17
- *Predaea masonii* (Setch. & Gard.) DeToni — 14

Rhodymeniales

- *Agardhinula browneae* (J. Agardh) DeToni — 9
- *Gloioderma atlantica* Searles — 13, 14, 17
- *Botryocladia occidentalis* (Børgesen) Kylin — 14, 16, 17
- *Botryocladia pyriformis* (Børgesen) Kylin — 17

Ceramiales

- *Antithamnion cruciatum* (C. Agardh) Nägeli — 3
- *Antithamnion cruciatum* var. *radicans* (J. Agardh) Collins & Hervey — 12, 13, 14, 17
- *Apoglossum ruscifolium* (Turner) J. Agardh — 17
- *Branchioglossum prostratum* Schneider — 13, 14, 16, 17
- *Ceramium byssoideum* Harvey — 3
- *Ceramium diaphanum* (Lightfoot) Roth — 1
- *Chondria tenuissima* (Goode. & Woodw.) C. Agardh — 8
- *Compsothamnion thuyoides* (Smith) Schmitz — 12, 13, 16, 17
- *Griffithsia tenuis* C. Agardh — 14, 16, 17, 18
- *Heterosiphonia wurdemanni* (Bailey *ex* Harvey) Falkenberg var. *laxa* Børgesen — 12, 17

Membranoptera subtropica Schneider	12, 13, 14, 16
Nitophyllum wilkinsoniae Collins & Harvey	12, 13
Polysiphonia tepida Hollenberg	3
Polysiphonia sphaerocarpa Børgesen	3
Pterosiphonia pennata (Roth) Falkenberg	3
Spermothamnion investiens (Crouan) Vickers var. *cidaricola* Børgesen	13, 17
Spyridia hypnoides (Bory) Papenfuss	2

DISCUSSION

The above list of 31 new records of red algae from South Carolina nearly doubles the list of rhodophycean taxa known from this region. About 200 taxa of red algae have been reported from North Carolina, South Carolina, and Georgia with most of these records from North Carolina. The above list of 35 taxa of reds previously reported, and the present list of 31 new records for South Carolina, a total of 66, belies what really is the red algal flora of the state. More intensive collecting should markedly expand the list.

The delesseriaceous species *Apoglossum ruscifolium* known only from Europe, the Falkland Islands, and the Atlantic coast of Argentina is newly reported from the western North Atlantic. *Spermothamnion investiens* var. *cidaricola*, described by Børgesen from the West Indies, is reported for the first time from the Carolinas. The following taxa have previously been reported only from North Carolina: *Gloioderma atlantica, Branchioglossum prostratum, Membranoptera subtropica.*

ACKNOWLEDGEMENTS

We would like to thank Dr. R. B. Searles of Duke University for providing offshore dredge collections made from the R/V *Eastward.* This cruise was made possible by NSF Grants GB-27725 and CG-00005 to the Duke University Cooperative Oceanographic Program. The first coauthor would also like to thank Dr. Searles for providing facilities for study in the Botany Department of Duke University.

REFERENCES

BAILEY, J. W. 1848. Continuation of the list of localities of algae in the United States. Am. J. Sci. & Arts 6: 37-42.

————. 1851. Microscopical observations made in South Carolina, Georgia and Florida. Smithson. Contr. Knowl., 2: 48 pp.

FARLOW, W. G. 1876. List of the marine algae of the United States. Dept. U.S. Comm. Fish and Fisheries for 1873-1874 and 1874-1875. pp. 691-718.

HARVEY, W. H. 1852-1858. Nereis Boreali-Americana. I. Melanospermeae. Smithson. Contr. Knowl., 3(4): 1-150, 1852; II. Rhodospermeae, *Ibid.*, 5(5): 1-258, 1853; III. Chlorospermeae, including supplements, *Ibid.* 10: ii + 1-140, 1858.

HOYT, W. D. 1920. Marine algae of Beaufort, N.C. and adjacent regions. Bull. Bur. Fish. (U.S.), 36: 367-556.

JORDAN, D. S. 1874. A key to the higher algae of the Atlantic coast between Newfoundland and Florida. Am. Nat. 8: 398-403.

MELVILL, J. C. 1875. Notes on the marine algae of South Carolina and Florida. J. Bot. Lond. 4: 258-265.

PEARSE, A. S. & L. G. WILLIAMS. 1951. The biota of the reefs off the Carolinas. J. Elisha Mitchell Sci. Soc. 67: 133-161.

SCHNEIDER, C. W. 1975. North Carolina marine algae. VI. Some Ceramiales (Rhodophyta), including a new species of *Dipterosiphonia*. J. Phycol 11: 391-396.

———— & R. B. SEARLES. 1976. North Carolina marine algae. VII. New species of *Hypnea* and *Petroglossum* (Gigartinales) and additional records of other Rhodophyta. Phycologia. 15(1): 51-60.

STEPHENSON, T. A. & A. STEPHENSON. 1952. Life between the tidemarks in North America. II. Northern Florida and the Carolinas. J. Ecol. 40: 1-49.

TAYLOR, W. R. 1957. Marine algae of the northeastern coast of North America. Revised ed. Univ. of Mich. Ann Arbor. viii + 509 pp.

————. 1960. Marine algae of the eastern tropical and subtropical coasts of the Americas. Univ. of Mich. Ann Arbor. ix + 870 pp.

ZANEVELD, J. S. 1966. The Marine Algae of the American Coast between Cape May, N.J. and Cape Hatteras, N.C. I. The Cyanophyta. Bot. Mar. 4: 101-128.

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A VEGETATION ANALYSIS OF THE GEORGIA FALL-LINE SANDHILLS

W. Z. Faust

Extending along the physiographic fall-line from central North Carolina to Alabama is a narrow belt of intermittent ridges and hills. These hills, which are made up of whitish or yellowish sands, are called the fall-line sandhills. The sandhills form an important physiographic feature through Georgia, South Carolina, and into North Carolina (Austin, 1965). The sandy ridges are higher than both the Coastal Plain on one side and the Piedmont region on the other side; elevation ranges from 30 to 50 feet (Hopkins & Hebb, 1954). The depth of the nearly pure sand is unknown, but it effectively protects the underlying clay or rocks from erosion. Soil permeability and internal drainage are rapid, and moisture retention for plant use is low (Burns & Hebb, 1972).

The vegetation of the xeric sandhills was once predominantly longleaf pine (Wells & Shunk, 1931). However, the lumber industry of the early 1900's removed most of the stands of longleaf pine and the understory scrub oaks assumed dominance because they adapted well to the droughty, acid sands (Burns & Hebb, 1972). Harper (1906), in his phytogeographical investigation of the Altamaha Grit region of the Coastal Plain of Georgia, included a brief discussion of the sandhills and a check-list of plants from different sandhill areas. He found *Quercus laevis* Walt. to be the dominant scrub oak and *Eriogonum tomentosum* Michx. the most abundant herb. An ecological study of the coarser sands of the North Carolina Coastal Plain was made by Wells and Shunk (1931). They reported on the vegetation and habitat factors and suggested that the flora of the sandhills is probably determined by nutrient and water factors and their relationship to root growth. Alien roots must grow rapidly through the relatively sterile sands to reach richer, moister

layers below. The Florida sandhills are covered by a longleaf pine-turkey oak association that forms open, park-like stands with abundant herbaceous ground-cover composed mostly of wire-grasses (Laessle, 1958). Duke (1961) made a floristic study of the Carolina fall-line sandhills and enumerated the xerophytic elements of the sandhill flora.

The objectives of this study were to determine the composition of the longleaf pine-scrub oak stands in the western portion of Georgia and to observe the ecology of the area.

DESCRIPTION OF THE STUDY AREA

The fall-line in Georgia runs through the central part of the state from Columbus, through Macon, to Augusta. The sandhills are very prevalent along the western portion of the fall-line east of Columbus in Talbot County. Numerous xeric, sandy ridges with unusual vegetation occur around Junction City, a small, rural community in Talbot County.

The sandhills selected for study are located between Geneva and Junction City along highway 80, and south of Junction City along highway 90. The high, dry hills with longleaf pine-scrub oak vegetation are common along both sides of the highways for many miles. The width of the sandhill belt is variable. Around Junction City, however, it seems to be about 20 miles wide. The longleaf pine-scrub oak stands are bordered on the north and south by loblolly-shortleaf pine stands and mixed pine-hardwood forests. As the vegetation of the sandhills changes to the pine and pine-hardwood stands, there is a noticeable difference in elevation and soil type as well.

The soils of the fall-line sandhills are acid in reaction and infertile. Results from this investigation indicate a soil pH range of 4.0-5.6. Brendemuehl (1967) reported that the pH of the sandhills ranged from 4.2-5.6, and the amount of organic matter was less than 2.0 per cent. The organic matter present on the surface of the sands oxidizes

quickly and released nutrients are leached from the upper strata by rain (Burns & Hebb, 1972). The soils also contain less than 10 per cent silt and clay. The loose, sandy soils produce much heat by reradiation; this affects micro-atmospheric temperature and a concomitant increase in evapotranspiration of surface moisture is likely. The sub-surface temperatures of soils are kept low by the reradiation of heat and this tends to conserve available water.

METHODS

The vegetation of the sandhills was analyzed by the quarter method of Cottam and Curtis (1956). After general reconnaissance in the study area, two representative sites were selected for intensive study. A total of 50 points (25 at each site) was sampled. Trees over four inches d.b.h. and saplings under four inches d.b.h. were scored, and shrubs and herbs were collected within the study area several times during the growing season. Tree seedlings at each sample point were identified to ascertain possible successional trends. A LaMotte soil test kit was used to check soil samples for pH. Voucher specimens were collected and deposited in the Columbus College Herbarium.

RESULTS

Information obtained by the quarter method of sampling is presented in Table 1 and the categories of Cottam and Curtis (1956) are used. The number of trees over four inches d.b.h. and the number of saplings under four inches d.b.h. are shown along with the following values for the trees and saplings: relative density, relative dominance, relative frequency, and importance values. The sandhill vegetation is dominated by turkey oak (*Quercus laevis*). Of the 200 trees scored, 175 were turkey oak, and of the 200 saplings scored, 159 were turkey oak. The importance values for turkey oak trees and saplings are 239.6 and 220.2 respectively out of a possible 300. Scrubby post oak (*Q. margaretta* Ashe) and bluejack oak (*Q. incana* Bartr.) are species of secondary importance. Of the 200 trees

TABLE 1. Importance Values of Trees and Saplings on the Sandhills in Talbot County, Georgia

	Number		*Relative Density*		*Relative Dominance*		*Relative Frequency*		*Importance Values*	
	Trees	Saplings	Trees	Saplings	Trees	Saplings	Trees	Saplings	Trees	Saplings
Quercus laevis	175	159	87.5	79.5	83.6	82.6	68.5	58.1	239.6	220.2
Quercus margaretta	12	10	6.0	5.0	5.5	5.1	13.7	11.0	25.2	21.1
Quercus incana	1	24	0.5	12.0	1.2	9.4	1.4	22.7	3.1	44.1
Quercus marilandica	2	0	1.0	0.0	0.9	0.0	2.7	0.0	4.6	0.0
Pinus palustris	6	0	3.0	0.0	6.9	0.0	8.2	0.0	18.1	0.0
Nyssa sylvatica	2	5	1.0	2.5	0.9	2.6	2.7	5.8	4.6	10.9
Diospyros virginiana	2	1	1.0	0.5	0.9	0.1	2.7	1.2	4.6	1.8
Pinus taeda	0	1	0.0	0.5	0.0	0.3	0.0	1.2	0.0	2.0

sampled, only six were longleaf pine (*Pinus palustris* Mill.); no longleaf pine saplings were scored in the quarter method. However, longleaf pine seedlings and saplings were observed along the edges of the scrub oak stands and in the areas where the oak canopy had been disturbed. *Nyssa sylvatica* Marsh. and *Diospyros virginiana* L. are broad-leaved taxa of lesser importance.

The shrubs associated with the scrub oak stands are numerous. The most abundant species are: *Asimina parviflora* (Michx.) Dunal, *Cornus florida* L., *Crataegus flava* Aiton, *C. uniflora* Muenchh., *Gaylussacia dumosa* (Andrz.) T. & G., *Myrica cerifera* L., *Prunus angustifolia* Marsh., *P. serotina* Ehrhart, *Rhus copallina* L., *R. toxicodendron* L., *Rubus cuneifolius* Pursh, *Sassafras albidum* (Nutt.) Nees, *Vaccinium arboreum* Marsh., *V. stamineum* L., and *V. tenellum* Aiton. Species of *Crataegus, Vaccinium,* and *Rhus* are the most common. *Myrica cerifera* is not as common on the sandhills as it is in the adjacent loblolly-shortleaf pine forests; it is found only in open areas that are lower and more mesic than the high, dry sites.

Herbaceous plants are present on the sandhills, but are not especially numerous. Duke (1961) stated that the grasses, composites, and legumes were the best represented groups on the xeric, sandy ridges. Species noted within these families include *Aristida stricta* Michx., *Andropogon scoparius* Michx., *A. ternarius* Michx., *A. virginicus* L., *Panicum* spp., *Erigeron strigosus* Michx. ex Willd., *E. canadensis* L., *Krigia virginica* (L.) Willd., *Liatris secunda* Ell., *L. tenuifolia* Nutt., *Vernonia angustifolia* Michx., *Baptisia cinerea* (Raf.) Fernald & Schubert., *B. perfoliata* (L.) R. Brown, *B. tinctoria* (L.) R. Brown, *Lespedeza* spp., and *Tephrosia virginiana* (L.) Pers. Other common xerophytic herbs are *Yucca filamentosa* L., *Asclepias humistrata* Walt., *Cnidoscolus stimulosus* (Michx.) Engelm. and Gray, and *Lithospermum caroliniense* (J. F. Gmelin) MacM. Ferns present include *Asplenium platyneuron* (L.) Oakes, *Polystichum acrostichoides* (Michx.) Schott, and *Pteridium aquilinum* (L.) Kuhn.

DISCUSSION

The vegetation of the Georgia fall-line sandhills is much like that of the turkey oak barrens of the Carolinas described by Duke (1961). In Talbot County, turkey oak dominates the vegetation and longleaf pine persists along the edges of the stands and in open areas. The scattered longleaf pines are reproducing by seed as evidenced by the number of young seedlings and saplings present, but the almost complete occupation by scrub oaks has prevented their re-establishment. The dense root systems of the scrub oaks and woody shrubs prevent the development of longleaf pine roots, while the diminished quality of light reaching the ground through the canopy of oaks and shrubs retards the growth of longleaf pine seedlings. The exclusion of fire on the sandhills has also added to the decline of longleaf pine.

In the Carolinas, the presence of *Quercus incana, Q. margaretta*, and *Q. marilandica* indicate more mesic forest conditions than does dominance by *Q. laevis* (Duke, 1961). The turkey oak stands in the western portion of Georgia, therefore, suggest more xeric conditions than the Carolina sandhills and a greater similarity to the Florida scrub oak areas. The number of turkey oak saplings indicates the species will maintain its dominance and not be replaced by the more mesophytic oaks.

LITERATURE CITED

AUSTIN, M. E. 1965. Land resource regions and major land resource areas of the United States. USDA Soil Conserv. Serv. Agric. Handbook 296. 82p.

BERGEAUX, P. J. 1968. Soils and fertilizers in Georgia. Univ. of Georgia College of Agric. and USDA Bulletin 656. 103p.

BRENDEMUEHL, R. H. 1967. Research progress in the use of fertilizers to increase pine growth on the Florida sandhills, pp 191-196. *In:* Forest fertilization . . . theory and practice symposium. Tenn. Val. Auth., Muscle Shoals, Ala.

BURNS, R. M. & E. A. HEBB. 1972. Site preparation and reforestation of droughty, acid sands. USDA Forest Serv. Agric. Handbook 426. 61p.

COTTAM, G., & J. T. CURTIS. 1956. The use of distance measures in phytosociological sampling. Ecology **37**: 451-460.

DUKE, J. A. 1961. The psammophytes of the Carolina fall-line sandhills. Jour. of the Elisha Mitchell Sci. Soc. **77**: 3-25.

HARPER, R. M. 1906. A phytogeographical sketch of the Altamaha Grit region of the coastal plain of Georgia. Ann. N.Y. Acad. Sci. **17**: 14-89.

HOPKINS, W., & E. A. HEBB. 1954. Guide to Chipola Experimental Forest. USDA Forest Serv. South. Forest Exp. Sta. 24p.

LAESSLE, A. M. 1958. The origin and successional relationships of sandhill vegetation and sand-pine scrub. Ecol. Mon. **28**: 361-387.

WELLS, B. W., & I. M. SHUNK. 1931. The vegetation and habitat factors of the coarser sands of the North Carolina coastal plain: an ecological study. Ecol. Mon. **1**: 465-520.

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A CYTOTAXONOMIC STUDY IN SOME SPECIES OF DROSERA

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The genus *Drosera* L. (family Droseraceae), with world-wide distribution, consists of approximately ninety species. About sixty species are concentrated in Australia. The basic classification of the family was established by Diels (1906) under the Englerian system. Behre (1929) tried to clarify relationships among the genera and species of the Droseraceae using karyological methods with a few species from *Dionaea* Ellis, *Drosera,* and *Drosophyllum* Link., but he found little evidence regarding relationships within the family. Although chromosome studies of some *Drosera* species have been made by various authors (e.g., Rosenberg, 1903, 1904, 1909; Shimamura, 1941; Wood, 1955; Kondo, 1966, 1969, 1970, 1971a, 1971b, 1971c, 1973), many more chromosome data are necessary to justify Diels' classification of the Droseraceae biosystematically, and to clarify species relationships.

The chromosome numbers of six species of *Drosera* are here reported for the first time. Two cytotypes of *Drosera spathulata* Labill. listed here differ from those which have been published previously (Kondo, 1971b). Also, cytotaxonomic relationships in *Drosera* are reviewed and discussed in relation to Diels' classification of *Drosera* (1906).

MATERIALS AND METHODS

Materials used in this study were acquired from the following sources:

Drosera cuneifolia L. f. — cultivated by J. A. Mazrimas, Livermore, California (native to Capeland, South Africa). The voucher specimen is deposited in the Herbarium of Kondo Collection, Nagoya.

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Drosera gigantea Lindl. — cultivated by J. A. Mazrimas (native to Western Australia, Australia). The voucher specimen is deposited in the Herbarium of Kondo Collection, Nagoya.

Drosera hamiltonii C. Andrews — cultivated by J. A. Mazrimas (native to Western Australia). The voucher specimen is deposited in the Herbarium of Kondo Collection, Nagoya.

Drosera neocaledonica Hamet — cultivated by J. A. Mazrimas (native to New Caledonia). The voucher specimen is deposited in the Herbarium of Kondo Collection, Nagoya.

Drosera petiolaris R. Br. — cultivated by J. A. Mazrimas (native to Western Australia, Northern Territory, and Queensland, Australia, and New Guinea). The voucher specimen is deposited in the Herbarium of Kondo Collection, Nagoya.

Drosera spathulata Labill. The Kanto cytotype — Ichimiya, Ichimiya-cho, Chosei-gun, Chiba Prefecture, Kanto District, Japan (collected by *S. Mori,* s.n., May 1973; sent by I. Kusakabe, Tokyo). The Yakushima cytotype — Yakushima Is., Kyushu District, Japan (collected by *K. Suzuki,* date unknown; sent by I. Kusakabe). The voucher specimens are deposited in the Herbarium, Department of Botany, The University of North Carolina, Chapel Hill (NCU).

Drosera adelae F. Muell — cultivated by D. E. Schnell, Statesville, North Carolina (native to a small area in Queensland, Australia). The voucher specimen is deposited in the Herbarium of Kondo Collection, Nagoya.

Root tips were fixed in Farmer's fluid. Chromosome preparations were made by the acetocarmine squash method. The symbols for the karyotype descriptions for *Drosera* are as follows: L = long chromosomes (longer than 2.5 μm), M = medium chromosomes (2.4-1.0 μm), S = short chromosomes (shorter than 1.0 μm), and sm = submedian constrictions.

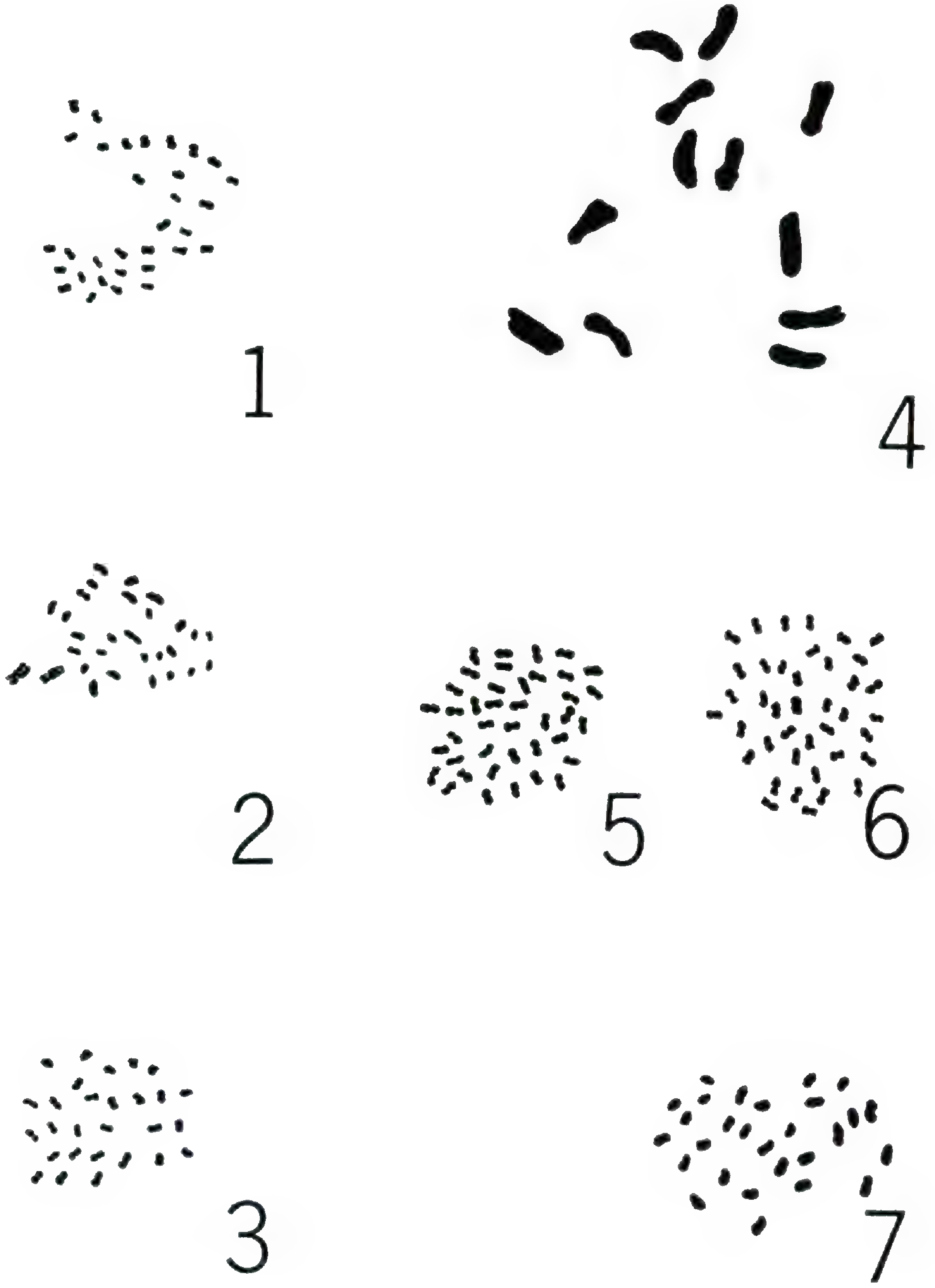

Fig. 1-7. Somatic chromosomes (x ca. 1450) of six species of *Drosera:* 1. *Drosera cuneifolia* L. f. (2*n* = 32); 2. *Drosera gigantea* Lindl. (2*n* = 28); 3. *Drosera hamiltonii* C. Andrews (2*n* = 28); 4. *Drosera petiolaris* R. Br. (2*n* = 12); 5. *Drosera spathulata* Labill. (Kanto cytotype; 2*n* = 40); 6. *Drosera spathulata* Labill. (Yakushima cytotype: 2*n* = 40); 7. *Drosera adelae* F. Muell. (2*n* = 28).

RESULTS AND DISCUSSION

Drosera cuneifolia has the somatic chromosome number $2n = 32$ (Fig. 1). The karyotype of the species is K $(2n = 32) = 32S$. Most of the chromosomes are the same in size (Fig. 9). Since the karyotype of the species is symmetrical in the tetraploid type, the basic chromosome number of it may be $x = 8$. This species is placed in subgenus *Rorella,* section *Rossolis,* series *Eurossolis* (Table 1). Species studied in this series show a basic chromosome number $x = 10$, which is different from that of *D. cuneifolia* $(x = 8)$.

Drosera neocaledonica and *D. spathulata* are also placed in the same section as the above. The karyotype of *Drosera neocaledonica is* K $(2n = 40) = 40S$. Most of the chromosomes are the same in size. Two cytotypes of *Drosera spathulata* (the Kanto cytotype, and the Yakushima cytotype) show the same somatic chromosome number: $2n = 40$ (Fig. 5, 6). The karyotypes of both cytotypes of *Drosera spathulata* are identical: K $(2n = 40) = 40M$. The idiograms of *Drosera spathulata* (Fig. 13, 14) show all the chromosomes for both cytotypes as essentially the same in size. The karyotypes and chromosome numbers presented here are the same as those reported for Australian tetraploid *Drosera spathulata.* The karyotype symmetry indicates that these three cytotypes, the Kanto cytotype, the Yakushima cytotype, and the Australian tetraploid cytotype, have an autotetraploid origin. Among the cytotypes of *Drosera spathulata,* the tetraploid cytotype might have the greatest distribution in Asia and Australia. These karyotypes and chromosome numbers are quite different from those of the Kansai cytotype of *Drosera spathulata,* in which K $(2n = 60) = 18L + 42S$ (Kondo, 1973). The Kansai cytotype of *Drosera spathulata* might be an allohexaploid. Thus, in Japan there are three cytotypes of *Drosera spathulata,* the Kansai cytotype, the Kanto cytotype, and the notable Kobayashi's *D. spathu-*

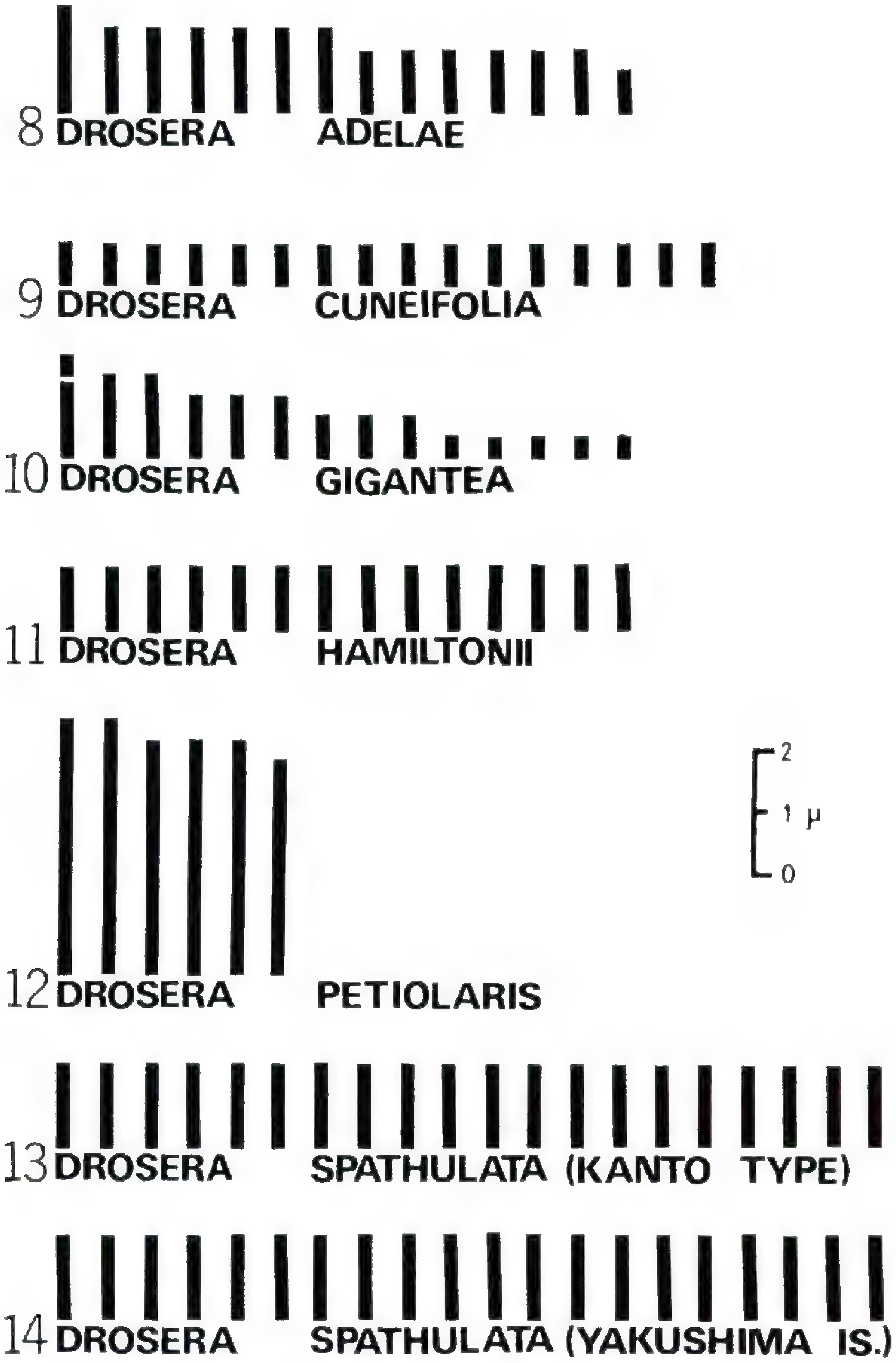

Fig. 8-14. Idiograms of six species of *Drosera:* 8. *Drosera adelae* F. Muell; 9. *Drosera cuneifolia* L. f.; 10. *Drosera gigantea* Lindl.; 11. *Drosera hamiltonii* C. Andrews; 12. *Drosera petiolaris* R. Br.; 13. *Drosera spathulata* Labill. (Kanto cytotype); 14. *Drosera spathulata* Labill. (Yakushima cytotype).

lata of hybrid origin (Kobayashi, 1950). The basic chromosome number x = 10 is typical of series *Eurossolis.*

Drosera gigantea, D. hamiltonii, and *D. adelae* show the same somatic chromosome number $2n = 28$ (Fig. 2, 3, 7). The karyotypes of the three species are as follows: *Drosera gigantea,* K $(2n = 28) = 2M^{sm} + 4M + 22S$; *D. hamiltonii,* K $(2n = 28) = 28S$; and *D. adelae,* K $(2n = 28) = 14M + 14S$.

Although the chromosome numbers of these three species are the same, their karyotypes differ and this indicates that each is of a distinct series. The karyotype of *Drosera gigantea,* which is symmetrical (Fig. 10) as a diploid, suggests it is a diploid series originating from an allotetraploid form, and its basic chromosome number might be x = 14. The basic chromosome number of *Drosera hamiltonii* might be x = 7, since its karyotype is symmetrical (Fig. 11) as a tetraploid. *Drosera adelae* shows a very symmetrical karyotype as a diploid (Fig. 8), and its basic chromosome number might be x = 14, instead of x = 7. *Drosera indica,* which is closely related to *D. adelae,* has fourteen bivalent chromosomes in meiosis (Kondo, 1966). This evidence suggests that the basic chromosome number for both *Drosera adelae* and *D. indica* might be x = 14. Thus, *Drosera gigantea* is placed in subgenus *Ergaleium,* section *Polypeltes,* for which the basic chromosome numbers 8, 10, 13, and 14 have been reported; *D. hamiltonii,* in subgenus *Rorella,* section *Stelogyne,* which has the reported basic chromosome number x = 7 (or 14); and *D. adelae,* in subgenus *Rorella,* section *Arachynopus,* which has the reported basic chromosome number x = 14.

Drosera petiolaris showed the largest chromosomes (Fig. 12; K $(2n = 12) = 12L$) which have ever been seen in the genus *Drosera,* and the somatic chromosome number is $2n = 12$ (Fig. 4), which is the lowest number in the genus. This is interesting because this number is the same as that of *Drosophyllum lusitanicum* Link. of the Droseraceae ($2n = 12$; Rothfels, *et al.,* 1968).

Table I. Basic chromosome numbers studied and Diels' classification of *Drosera*

Taxa	Basic chromosome number
Drosera	
Subgenus I. *Rorella* DC.	
Section I. *Psychophila* Planch.	10
Section II. *Bryastrum* Planch.	unknown
Section III. *Lamprolepis* Planch.	unknown
Section IV. *Thelocalyx* Planch.	10
Section V. *Coelophylla* Planch.	unknown
Section VI. *Arachynopus* Planch.	14
Section VII. *Rossolis* Planch.	
Series I. *Eurossolis* Diels	8, 10
Series II. *Lasiocephala* Planch.	6
Section VIII. *Stelogyne* Diels	7
Section IX. *Phycopsis* Planch.	8
Subgenus II. *Ptycnostigma* Planch.	
Section X. *Ptycnostigma* Planch.	unknown
Subgenus III. *Ergaleium* DC.	
Section XI. *Polypeltes* Diels	8, 10, 13, 14
Section XII. *Erythrorrhiza* Planch.	7 or 14

Table I shows the basic chromosome numbers reported for the sections and series in Diels' classification of *Drosera*. The basic chromosome number x = 10 is more common, being found in four of the sections studied and in a polyploid series in *Drosera*. Although *Drosera cuneifolia* is placed in subgenus *Rorella*, section *Rossolis*, series *Eurossolis*, which is mostly a polyploid series with the basic chromosome number of ten, it has the somatic chromosome number $2n = 32$. Thus, the chromosome number of *Drosera cuneifolia* might have originated from the basic chromosome number of ten by some kind of chromosome

aberration ($2n = 30 + 2$). Subgenus *Rorella,* section *Rossolis,* series *Lasiocephala* is represented by *Drosera petiolaris,* which has the lowest chromosome number, $2n = 12$, and larger chromosomes in size than those of any other species in the genus. However, this suggests that this species might be the most primitive species in the genus. The basic chromosome number $x = 7$ is found in one section, subgenus *Rorella,* section *Stelogyne,* which is closely related to section *Rossolis.* The basic chromosome number $x = 7$ might have originated from $x = 6$. In contrast, the section *Arachnopus,* which is considered to be morphologically more primitive than some other sections, has the basic chromosome number $x = 14$ which might have originated as an allotetraploid form; in other words, the basic chromosome number $x = 14$ might result from a hybrid origin ($8 + 6$).

Drosera pedata Pers. has the somatic chromosome number $2n = 32$ and the basic chromosome number $x = 8$. This binomial is a synonym of *Drosera binata* Labill. which belongs to subgenus *Rorella,* section *Phycopsis* (Diels, 1906). The somatic chromosome number of *Drosera binata* is $2n = 46$ which is quite different from that of *D. pedata.* However, the somatic chromosome number $2n = 46$ of *Drosera binata* might be the result of a hybrid origin (Sato, 1948; $32 + 16$) and reduction (Kress, 1970; $48 - 2$). Thus, the basic chromosome number of section *Phycopsis* might be $x = 8$. Sato (1948) also states that the chromosome number of *Drosera regia* Stephens ($2n = 34$) might be of hybrid origin, but it would be more natural to consider that the chromosome number of *D. regia* might have originated from chromosome doubling ($8 \times 2 = 16$) and increase ($16 + 1 = 17$) since hybridization between *D. regia* and other species is almost impossible. Subgenus *Ergaleium,* section *Polypeltes* which has various basic chromosome numbers ($x = 8, 10, 13, 14$), indicates this group might not be stabilized yet, with aneuploidy more common than in the other groups. The basic chromosome number $x = 14$ might be an allotetraploid source, and

x = 13 might have originated from 14 by chromosome reduction.

Additional cytological observations of other species of *Drosera* could be expected to improve our concept of the interrelationships among species of *Drosera*.

ACKNOWLEDGMENT

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LITERATURE CITED

BEHRE, K. 1929. Physiologische und zytologische Untersuchungen über *Drosera*. Planta **7**: 208-306.

DIELS, L. 1906. Droseraceae: *In* A. Engler, Das Pflanzenreich IV, 112.

KOBAYASHI, S. 1950. Evidence for the hybrid origin of *Drosera spathulata* (in Japanese): Abstract for the 1950 Annual Meeting of the Botanical Society of Japan. Bot. Mag. Tokyo **63(749)**: 227.

KONDO, K. 1966. Meiosis in PMC of three species of *Drosera*. Chromosome Inf. Serv. **7**: 23-24.

————. 1969. Chromosome numbers of carnivorous plants. Bull. Torrey Bot. Club **96**: 322-328.

————. 1970. Chromosome numbers in *Drosera* and *Dionaea* in North Carolina. Journ. Jap. Bot. **45**: 139-144.

————. 1971a. Chromosome number of *Drosera burmanni* Vahl from Borneo. Journ. Jap. Bot. **46**: 160.

————. 1971b. A review of the *Drosera spathulata* complex. Journ. Jap. Bot. **46**: 321-326.

————. 1971c. Chromosome number of *Drosera arcturi* Hook. (with B. Whitehead). Journ. Jap. Bot. **46**: 344.

————. 1973. Chromosome numbers of some *Drosera* taxa. Journ. Jap. Bot. **48**: 193-198.

KRESS, A. 1970. Zytotaxonomische Untersuchungen an einigen Insektenfängern (Droseraceae, Byblidaceae, Cephalotaceae, Roridulaceae, Sarraceniaceae). Ber. Dtsch. Bot. Ges. **83(2)**: 55-62.

ROSENBERG, O. 1903. Das Verhalten der Chromosomen in einer hybriden Pflanze. Ber. Dtsch. Bot. Ges. **21**: 110-119.

————. 1904. Über die Tetradenteilung eines *Drosera* — Bastardes. Ber. Dtsch. Bot. Ges. **22**: 47-53.

———. 1909. Cytologische und morphologische Studien an *Drosera longifolia* × *rotundifolia*. K. Svenska Vet. Akad. Handl. N. S. 43: 1-65.

ROTHFELS, K., & M. HEIMBURGER. 1968. Chromosome size and DNA value in sundews (Droseraceae). Chromosoma 25: 96-103.

SATO, D. 1948. The karyotype of the insectivorous plants. Oguma Comm. Vol. Cytol. Genet.: 25-28.

SHIMAMURA, T. 1941. Cytological study of *Drosera obovata* Mert. et Koch with special reference to its hybridity. Bot. Mag. Tokyo 55: 553-558.

WOOD, C. E. 1955. Evidence for the hybrid origin of *Drosera anglica*. Rhodora 57: 105-130.

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A NEW SPECIES OF PANICUM (GRAMINEAE) FROM MOLOKAI. HAWAIIAN PLANT STUDIES 42

Harold St. John

On the north shore of Molokai Island, Hawaiian Islands, at Moomomi, there is a charming sandy beach. Since the trade winds sweep from the sea across the beach, dry sand grains are blown inland. Behind the beach they have formed an extensive area of sand dunes. Also the sands have been blown two miles inland and upland to the southwest to the divide at 600 feet altitude, and two miles beyond it down the western slope. Well inland the smaller dunes are more or less stabilized and the geologists call them consolidated calcareous dunes. All of this area is interesting botanically, and in it the native beach and psammophytic floras are well preserved. The present paper adds one species to its flora.

Gramineae

Panicum moomomiense sp. nov. (Fig. 1).

Diagnosis Holotypi: Plantae aggregatae vel solitariae (aspectu herbae annuae) 4-14 cm altae, erectae plerumque basi ramosae culmis simplicibus (raro supra ramosis); internodia 6-32 mm longa adpresse adscendente albo-pilosula vaginae 8-23 mm longae nervis multis parallelis elevatis glabris sed intervallis adscendente albo-puberulis; ligula albo-pilosa ad margines pilis 2 mm longis, ad centrum pilis 0.3-0.4 mm longis; folia basalia laminis 23-25 mm longis; folia caulina laminis 13-37 mm longis 0.8-1 mm latis sed forte involutis et primo viso 0.3-0.4 mm latis, supra dense adscendente albo-pilosa infra nervis parallelis glabris sed intervallis minutissime adscendente albo-puberulis; panicula terminalis 1.3-2.5 cm longa 2-3 mm lata exserta et 8-38 spiculas ferens, ramis paucis adpresse adscendentibus; rhachis rami et pedicelli adscendente albo-pilosi; pedicelli 0.5-3 mm longi; spiculae 1.2-1.5 mm longae glabrae

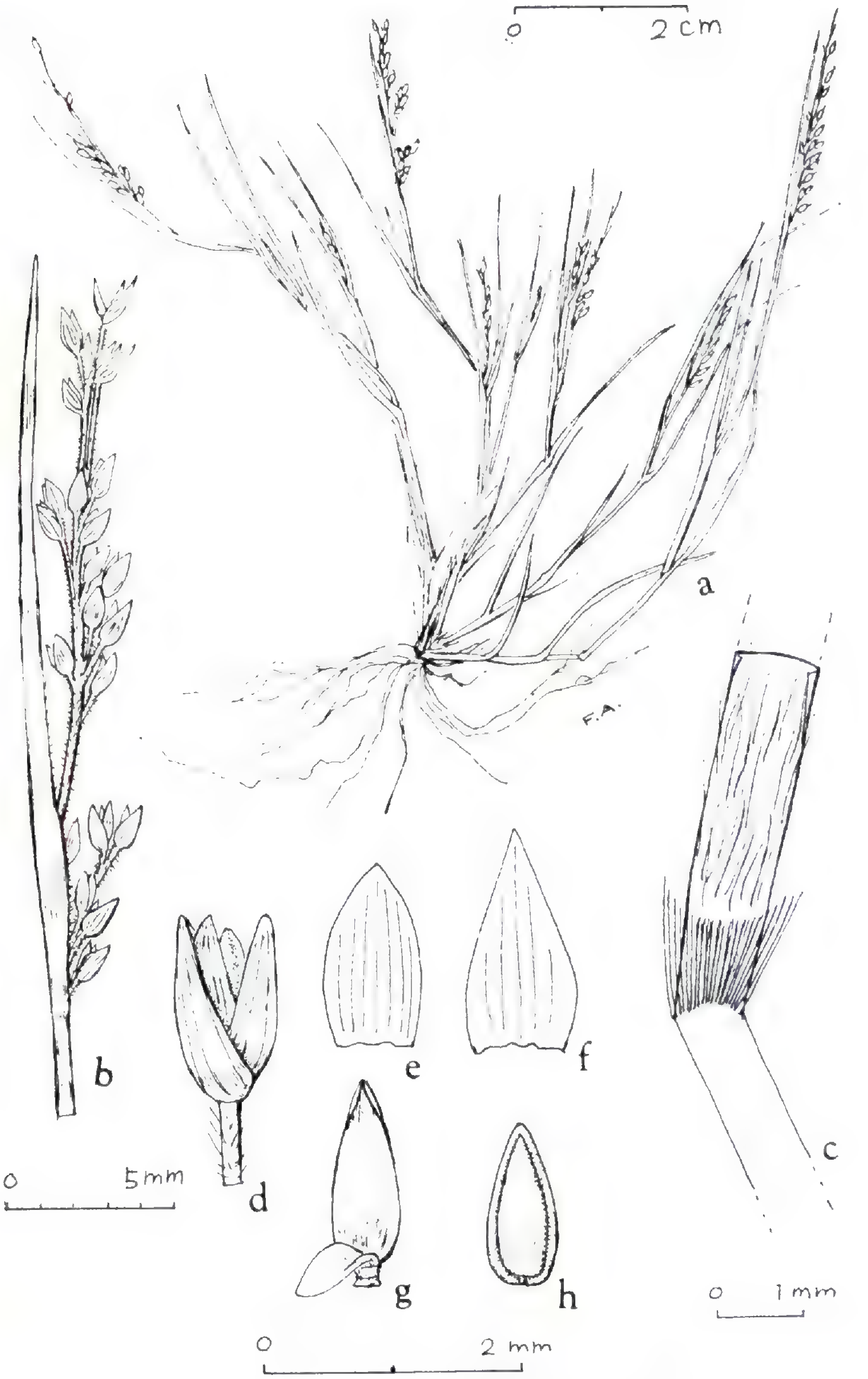

Fig. 1. *Panicum moomomiense* St. John, from holotype. *a*, habit, × 1; *b*, inflorescence, × 4; *c*, tip of sheath, ligule, and base of blade, × 10; *d*, spikelet, × 15; *e*, first glume, × 15; *f*, second glume, × 15; *g*, sterile lemma, × 15; *h*, fertile lemma and palea, × 15.

ellipsoideae acutae; gluma prima 1.2-1.4 mm longa, alias bracteas florales paulo excedens, ovata 5-nervosa nervis 3 centralibus elevatis obscure viridibus apicem forte attingentibus apiceque convergentibus et latere quoque nerva subtili apicem non attingenti; gluma secunda 0.9-1 mm longa ovata 7-nervosa; lemma sterilis 0.8-0.9 mm longa elliptica indistincte 5-nervosa; lemma fertilis 0.8 mm longa elliptica cartilaginea involuta 7-nervosa; palea 0.7-0.8 mm longa elliptica cartilaginea pallida; antherae 0.4 mm longae aurantiacae; stigmata obscure purpurea.

Diagnosis of Holotype: Plants in small tufts or single, (and appearing like an annual), 4-14 cm tall, erect, mostly several branched at base and the culms simple, (rarely branched above); internodes 6-32 mm long, appressed ascending white pilosulous; leaf sheaths 8-23 mm long, enclosing and concealing the culm, with numerous parallel raised glabrous nerves, but the concave intervals white ascending puberulous; ligule white pilose, at the margins with hairs 2 mm long, pilosulous, and the center with hairs 0.3-0.4 mm long; basal leaves with blades 23-55 mm long; cauline leaves with blades 13-37 mm long, 0.8-1 mm wide, but tightly involute and appearing 0.3-0.4 mm wide, above densely ascending white pilose, below with glabrous parallel nerves, but the intervals very minutely white ascending puberulous; panicle terminal, 1.3-2.5 cm long, 2-3 mm wide, exserted, bearing 8-38 spikelets, the few branches appressed ascending; rhachis, branches, and pedicels ascending white pilose; pedicels 0.5-3 mm long; spikelets 1.2-1.5 mm long, glabrous, ellipsoid, acute; first glume 1.2-1.4 mm long, slightly exceeding the other floral scales, ovate, 5-nerved, the 3 central ones raised, dark green, running strongly to and converging at the apex, on each side with one more lateral nerve, weak and not reaching the apex; second glume 0.9-1 mm long, ovate, 7-nerved; sterile lemma 0.8-0.9 mm long, elliptic, faintly 5-nerved; fertile lemma 0.8 mm long, elliptic, involute, 7-nerved, cartilaginous; palea 0.7-0.8 mm long, elliptic, cartilaginous, pale; anthers 0.4 mm long, orange; stigmas dark purple.

Holotypus: Hawaiian Islands, Molokai Island, Moomomi, limestone sand dune, 1 mile s. w. of beach, Jan. 21, 1973, *Noah Pekelo Jr.* 18 (BISH).

Specimens Examined: Hawaiian Islands, same data, Jan. 1, 1973, *Pekelo* 8 (BISH). Ilio Pt., sandy gravel, 2/28/74, *Pekolo* 30 (BISH).

Discussion: This new species is most closely related to *Panicum Fauriei* Hitchc. of Molokai and Hawaii, a species with the culms puberulent, branched at all the nodes, 10-15 cm tall; ligule a ciliate membrane with hairs nearly 1 mm long; cauline blades 2-5 cm long, flat or more or less involute, above appressed villous, below appressed hispidulous; spikelets 2 mm long; first and second glumes equal, lanceolate; second glume 5-nerved; sterile lemma 1.4 mm long, 5-nerved; fertile lemma 1.5 mm long. *P. moomomiense* has the culms ascending pilosulous, 4-12 cm tall, unbranched except at base; ligule white pilose, at the margins with hairs 1 mm long, and at the center with hairs 0.3-0.4 mm long; cauline blades 1.3-3.7 cm long, tightly involute; spikelets 1.2-1.4 mm long; first glume 1.2-1.4 mm long, ovate; second glume 0.9-1 mm long, ovate, 7-nerved; sterile lemma 0.8 mm long, 7-nerved; fertile lemma 0.8-0.9 mm long.

The writer has been unable to find a published section of the genus with characters that would include those of this species.

The new epithet is formed from the name of the type locality, Moomomi, and *-ense,* the Latin adjectival place ending.

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BAUHINIA LUNARIOIDES: A MISAPPLIED NAME[1]

RICHARD P. WUNDERLIN

Torrey (1859) described what he believed to be a new species of the caesalpinioid legume genus *Casparia* based on a fragmentary specimen collected by C. C. Parry from Mexico during the United States and Mexican boundary survey. His brief description is as follows: *Casparia, n. sp.? Rocky hills near Santa Rosa, Chihuahua; Parry. An erect shrub, 2-3 feet high. Branches slender, flexuous, smooth. Leaflets distinct to the base, semiovate, very obtuse. 3-nerved, very smooth. Pods (old and imperfect) about 2 inches long and one-third of an inch wide.*

Nineteen years later Watson (1878) published a manuscript name of Asa Gray, *Bauhinia lunarioides*, citing Torrey's description. This constituted valid publication of a new species of *Bauhinia*.

Recently a specimen was located in the Gray Herbarium which I have determined to be the holotype of *Bauhinia lunarioides* Gray ex Watson. The specimen consists of a sterile and apparently juvenile branch with fragments of an old fruit in the attached packet. The sheet, I believe, is unquestionably that from which Torrey wrote his description of the species. Label data written in pen with black ink conforms in part to that given by Torrey in his description: *Rocky hills near Santa Rosa, Jany* [sic, January] *1853. A shrub 2-3 feet high. Only vestiges of pods were found.* In the upper right corner of the label written in the same manner as the above is the number *2901a* and written in pencil near the top of the label in apparently the same hand is found: *Casparea* [*sic*], *n. sp.* — *Torr.* Comparison of handwriting on manuscripts at the Missouri Botanical Garden indicate that it appears to be that of C. C. Parry. However, written on the label in pencil and in an unknown hand is the name *Bauhinia.* Also written on

[1]Contribution no. 91 from the Botanical Laboratories of the University of South Florida, Tampa.

the sheet in pencil in a second unknown hand is *B. lunarioides Gray juvenile* and near the label and in pen with blue ink is *Coahuila: MEXICO.* Although a comparison of handwriting in the manuscript collection at the Missouri Botanical Garden did not reveal the identity of either of the latter two handwritings, all other evidence indicates that this sheet is the holotype specimen of *Bauhinia lunarioides* Gray ex Wats.

The species represented by the type specimen of *Bauhinia lunarioides* Gray ex Wats. is that which is going under the currently accepted name of *Bauhinia congesta* (Britt. & Rose) Lundell. The latter name must therefore be replaced with the earlier name *B. lunarioides.* The complete synonymy for this species is as follows:

Bauhinia lunarioides Gray ex Wats., Bibl. Ind. N. Amer. Bot. 205. 1878. TYPE: Mexico: Coahuila: *Parry* 2901a (HOLOTYPE: GH).

Casparia congesta Britt. & Rose, N. Amer. Fl. 23: 211. 1930. TYPE: Mexico: Coahuila: *Palmer* 285 (HOLOTYPE: US; ISOTYPES: LE, NY, P, VT).

Casparia jermyana Britt. in Britt. & Rose, N. Amer. Fl. 23: 211. 1930. TYPE: United States: Texas: *Jermy s.n.* (HOLOTYPE: NY).

Bauhinia congesta (Britt. & Rose) Lundell, Phytologia **1**: 214. 1937.

Bauhinia jermyana (Britt.) Lundell. Phytologia **1**: 214. 1937.

Further confusion was brought about by Britton and Rose (1930) when they subsequently described an entirely different species of *Bauhinia* which they unfortunately named *Casparia lunarioides,* again using a Gray manuscript name. These workers then compounded the confusion by incorrectly placing *Bauhinia lunarioides* Gray ex Wats. in synonymy under their new species. *Casparia lunarioides* Gray ex Britt. & Rose is now correctly placed in synonymy under *Bauhinia macranthera* Benth. ex Hemsl. and the complete synonymy for this species is as follows:

Bauhinia macranthera Benth. ex Hemsl., Diag. Pl. Nov. 49. 1880. TYPE: Mexico: Hidalgo: *Coulter s.n.* (HOLOTYPE: K, not seen).

Bauhinia retifolia Standl., Contr. U.S. Nat. Herb. 23: 416. 1922. TYPE: Mexico: San Luis Potosi: *Purpus* 5268 (HOLOTYPE: US; ISOTYPES: F, MO, NY, UC).

Casparia lunarioides Gray ex Britt. & Rose, N. Amer. Fl. 23: 212. 1930. TYPE: Mexico: Nuevo Leon: *Pringle* 2529 (HOLOTYPE: US; ISOTYPES: A, F, GH, MO, NY, P, UC, VT).

Casparia macranthera (Benth. ex Hemsl.) Britt. & Rose, N. Amer. Fl. 23: 212. 1930.

Casparia retifolia (Standl.) Britt. & Rose, N. Amer. Fl. 23: 213. 1930.

Bauhinia macranthera var. *grayana* Wunderlin, Phytologia **15**: 53. 1967.

My first interpretation of *Bauhinia macranthera,* based on herbarium study, was that it consisted of two varieties: var. *macranthera* and var. *grayana.* However, in recent field studies of this species I observed that the characteristics used in delimiting these taxa break down completely. Thus I now recognize only a single taxon.

LITERATURE CITED

BRITTON, N. L. & J. N. ROSE. 1930. Caesalpiniaceae. N. Amer. Fl. 23: 201-349.

TORREY, J. 1859. *In* W. H. Emory: Report on the United States and Mexican Boundary Survey. Botany of the Boundary 2(1): 29-270.

WATSON, S. 1878. Bibliographic Index of North American Botany. Smiths. Inst. Misc. Collect. 15: 1-476.

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TWO MEMBERS OF THE RUBIACEAE NEW TO OHIO[1,2]

E. LUCY BRAUN[3]

Since the publication of Edward J. P. Hauser's "Rubiaceae of Ohio" (1964) I have found two taxa not mentioned there — a *Galium* and a *Houstonia.*

Galium pedemontanum All. is a small inconspicuous European species with tiny yellow flowers and leaves in four's. The three more recent manuals — Fernald (1950), Gleason (1952), and Gleason and Cronquist (1963) — cite it as occurring in West Virginia and Kentucky. My Ohio specimen, from a grassy area in Anderson Township, Hamilton County, adds another state to the known range. I have also found it in Carter Caves State Park in Kentucky.

REPRESENTATIVE SPECIMENS: **Kentucky:** CARTER CO., Carter Caves State Park, dry slope (recently disturbed) above lake, May 21, 1964, *Braun* 4957 (US); same, May 20, 1964, s.n. (US). **Ohio:** HAMILTON CO., Newtown Road, Anderson Township, in grass, June 1, 1964, *Braun,* s.n. (US). (Additional vouchers are deposited at GH and NY.)

Although *Houstonia setiscaphia* L. G. Carr is reduced to synonymy with *H. canadensis* Willd. (Terrell, 1959), it seems desirable to note the occurrence of this plant in Ohio. Until now, it has been known only from Lee County, Virginia, the type locality, where it grows in "calcareous barrens and glades," and from adjacent Scott County (Natural Tunnel), where it was found clinging in crevices of limestone. Lee County occupies the extreme western angle of Virginia, and is in the Ridge and Valley Province of physiographers, near the eastern boundary of the Appalachian Plateau Province; the lower lands are limestone flats where rock may be exposed on the surface.

[1]Communicated by Dr. Margaret Fulford.

[2]The editor thanks Dr. F. Raymond Fosberg for supplying the specimen citations.

[3]Deceased March 5, 1971.

Our Ohio specimens, from Adams County, occur in a comparable situation — in the narrow band of Knobs along the western border of the Appalachian Plateau, the part referred to as Unglaciated Allegheny Plateau. The plant community in which *H. setiscaphia* occurs can be called cedar barrens, or open rocky xeric prairie. The plants are usually in the more open spots, rarely in crevices of very low cliffs. The exposed rocks are Peebles dolomite (Silurian).

REPRESENTATIVE SPECIMENS: **Ohio:** ADAMS CO., Lynx Prairie Preserve, open bare spots in prairie where dolomite at surface, May 20, 1967, *Braun*, s.n. (US); same, June 27, 1966, *Braun*, s.n. (US); "Lynx", Sept. 4, 1931, *Braun*, s.n. (US); Beaver Pond, open shale slopes, no date, *Braun*, s.n. (US); Peach Mt., oak woods, shale slope, May 20, 1924, *Braun*, s.n. (US).

Although similar to typical *Houstonia canadensis,* which also occurs here, *H. setiscaphia* is readily spotted in the field, both at initiation of flowering and later, because of its different aspect. Closer inspection reveals characters by which it differs: conspicuously scabrous or hispid angles of the stem, denser inflorescence, hispid calyx, smaller and more crowded flowers, and oblanceolate leaves.

Terrell noted the variability of *Houstonia canadensis* and to a lesser extent, of *H. setiscaphia,* and the overlapping of characters between them. Because the two taxa occur in the same community in Adams County, ecotypical variation may be ruled out.

A specimen from the Lynx Prairie Preserve (a Natural Landmark), sent to the Gray Herbarium, Harvard University, was compared with the type by Reed C. Rollins who states "I have compared your material with the type . . . and the specimens match very well."

The whole *Houstonia purpurea* species-complex, to which *H. canadensis* and *H. setiscaphia* belong, is made up of closely related and variable (sometimes intergrading) species. *Houstonia setiscaphia* may (perhaps correctly) be considered as only a variant of *H. canadensis;* however, its occurrence in Ohio should be noted in order that the geographic occurrence of these taxa may be studied further.

LITERATURE CITED

FERNALD, M. L. 1950. Gray's manual of botany, 8th ed. New York. American Book Co.

GLEASON, H. A. 1952. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. 3 vols. Lancaster, Pa., Lancaster Press.

————, & A. CRONQUIST. 1963. Manual of vascular plants of northeastern United States and adjacent Canada. D. Van Nostrand Co., Princeton, N. J.

HAUSER, J. P. 1964. The Rubiaceae of Ohio. Ohio Jour. Sci., 64: 27-35.

TERRELL, E. E. 1959. A revision of the *Houstonia purpurea* group (Rubiaceae). Rhodora 61:157-180, 188-207.

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THELYPTERIS LIMBOSPERMA IN EASTERN NORTH AMERICA

André Bouchard and Stuart G. Hay

Thelypteris limbosperma (All.) H.P. Fuchs was collected for the first time in eastern North America, on the west coast of Newfoundland, in July 1973. The fern was found growing along small streams in an open forest of *Abies balsamea*, in the tablelands of the Long Range Mountains.

The species, widely distributed in the northern hemisphere, has been notable in its absence from eastern North America. In North America, its distribution has been restricted to the Pacific coast, from coastal Alaska (including the Aleutian Islands) to southeast British Columbia and the Cascade Mts. of central Washington (Hitchcock et al., 1969).

The Eurasian distribution is more complex. The species is found in Central and North Western Europe extending from southern Sweden to the western Ukraine and south to Central Italy and the Pyrenees (Tutin et al., 1964). In Asia, apart from a few isolated localities in Siberia (Hultén, 1962), this fern is found from the Kamtchatka Peninsula to Honshu (Japan) — (refer to distribution map, Hultén, 1962).

Botanical and geological studies, subsequent to Fernald's proposal (1925) of unglaciated "nunatak" zones in northeastern North America, have been critical of this hypothesis whereby disjunct populations survived in refugia. Alternatively, if we presume that Newfoundland was completely glaciated during the Pleistocene and that all vegetation was destroyed, this population of *Thelypteris limbosperma* may be regarded as a postglacial introduction. Considering the isolation of the population and the absence of other localities in eastern North America, it may be concluded that the species was not introduced by man but instead owes its origin to long-distance dispersal from

either a Eurasian, a western North American, or a now extinct eastern North American population.

SPECIMENS: *Thelypteris limbosperma* (All.) H. P. Fuchs, St. Barbe South District: Heather Pond (P113); open *Abies balsamea* forest on wet slope with *Rhododendron canadense* and *Rubus chamaemorus*. Lat. 49° 46′ N, Long. 57° 33′ W., alt. 1650′. July 14, 1973. *Bouchard and Hay* 73-507, (BH, CAN, DAO, GH, MT).

ACKNOWLEDGEMENTS

The specimens of *Thelypteris limbosperma* were determined by Dr. D. M. Britton of the University of Guelph, Ontario, Canada. Dr. B. Boivin of the Canadian Department of Agriculture, Ottawa, and Dr. A. Tryon of the Gray Herbarium at Harvard University, have also seen the specimens.

Dr. D. M. Bates of Cornell University and Dr. E. Rouleau of the University of Montreal kindly revised the text of this brief communication.

LITERATURE CITED

FERNALD, M. L. 1925. Persistence of plants in unglaciated areas of boreal America. Mem. Amer. Acad. Arts 15: 238-342.

HITCHCOCK, C. L., A. CRONQUIST, M. OWNBEY, & J. W. THOMPSON. 1969. Vascular Plants of the Pacific Northwest: Part I. Univ. of Washington Press. 914 pp.

HULTÉN, E. 1962. The circumpolar plants. I. Kongl. Svenska Vetenskapsakad. Handl. IV, 8(5): 1-275.

TUTIN, T. G., J. H. HEYWOOD, N. A. BURGES, D. H. VALENTINE, S. M. WALTERS, & D. A. WEBB. 1964. Flora Europea. I. Cambridge University Press. 464 pp.

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DELPHINIUM VIRESCENS IN ALABAMA

Jerry M. Baskin and Carol C. Baskin

Delphinium virescens Nutt. (Ranunculaceae) is a polycarpic, herbaceous perennial that occurs throughout a large portion of the prairies and plains of the United States and extends into Manitoba, Canada (Ewan, 1945; Fernald, 1950; Gleason and Cronquist, 1963). Weaver and Fitzpatrick (1934) list it as a characteristic species of both upland and lowland prairies. In addition to its wide geographical distribution in the North American Grasslands, disjunct populations of the species occur in the cedar glades of central Tennessee (Quarterman, 1950; Baskin *et al.*, 1968; Baskin and Baskin, 1974) and northwestern Georgia (Baskin *et al.*, 1968).

Apparently *Delphinium virescens* has not been reported from Alabama. It is not listed by Mohr (1901) in his *Plant Life of Alabama* and neither Small (1933), Fernald (1950), nor Gleason and Cronquist (1963) include Alabama in their range descriptions of the species. In fact, Small (1933) and Fernald (1950) do not list it as occurring in the southeastern United States. Gleason and Cronquist (1963) include Louisiana alone of the Southeastern states in their range delineation. In a recent publication, which included several new state records for plants in Alabama, Kral (1973) made no mention of *D. virescens.*

The purpose of this communication is to report the occurrence of *Delphinium virescens* in Alabama. On 27 May, 1972, we found a small population of this species growing in shallow, limestone soil in Jackson County in northern Alabama (*Baskin & Baskin* 1317). The population is located along U.S. 72, 0.4 mile east of its intersection with Ala. 79. Plants associated with *D. virescens* at this locality included: *Arenaria patula* Michx. var. *patula, Senecio smallii* Britt., *Agave virginica* L., *Croton monanthogynus* Michx., *Houstonia lanceolata* (Poir.) Britt., *Ruellia humilis* Nutt., *Ophioglossum engelmanni* Prantl, *Opuntia compressa*

(Salisb.) Macbr., *Verbena simplex* Lehn., *Monarda fistulosa* L. and *Prunella vulgaris* L.

A voucher specimen of *Delphinium virescens* from the Alabama location has been sent to VDB.

LITERATURE CITED

BASKIN, J. M., E. QUARTERMAN & C. CAUDLE. 1968. Preliminary check-list of the herbaceous vascular plants of cedar glades. J. Tenn. Acad. Sci. **43**: 65-71.

————, & C. C. BASKIN. 1974. Some aspects of the autecology of prairie larkspur (*Delphinium virescens*) in Tennessee cedar glades. Amer. Midl. Natur. **92**: 58-71.

EWAN, J. A. 1945. Synopsis of the North American species of *Delphinium*. Univ. of Colorado Studies Ser. D, **2**: 55-244.

FERNALD, M. L. 1950. Gray's manual of botany. 8th Ed. Amer. Book Co., New York.

GLEASON, H. A. & A. CRONQUIST. 1963. Manual of vascular plants of northeastern United States and adjacent Canada. Van Nostrand Reinhold Co., New York.

KRAL, R. 1973. Some notes on the flora of the southern states, particularly Alabama and middle Tennessee. Rhodora **75**: 366-410.

MOHR, C. 1901. Plant life of Alabama. Contrib. U.S. National Herbarium. Vol. 6, Government Printing Office, Washington, D. C.

QUARTERMAN, E. 1950. Major plant communities of Tennessee cedar glades. Ecology **31**: 234-254.

SMALL, J. K. 1933. Manual of the southeastern flora. Univ. of N. C. Press, Chapel Hill.

WEAVER, J. E. & T. J. FITZPATRICK. 1934. The prairie. Ecol. Monogr. **4**: 109-295.

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REDISCOVERY OF VAUCHERIA NASUTA IN MASSACHUSETTS[1]

E. E. WEBBER

The genus *Vaucheria* is one of the most frequently encountered of the numerous cryptogamic plants (Webber & Wilce, 1971) common to New England salt marshes. Its turf-like growth habit on both muddy and marine peat substrates makes it a readily recognizable component of the marine algal vegetation.

Despite its prevalence, only four species of *Vaucheria* were known from the extensive tidal marshes in New England prior to 1953. At this time, four additional species were reported by Blum & Conover (1953) from the Woods Hole (Massachusetts) area, bringing the total number to eight. These eight species are: *Vaucheria compacta* (Collins) Collins; *V. litorea* C. Ag.; *V. piloboloides* Thur. (see, however, Blum, 1972, p. 29); *V. thuretii* Woron.; *V. arcassonensis* Dangeard; *V. coronata* Nord.; *V. intermedia* Nord.; and *V. minuta* Blum & Conover, as a new species. Shortly thereafter, a second new *Vaucheria* species, *V. vipera* Blum, was reported by Blum (1960) from a marsh at Essex, Massachusetts. Subsequently, at nearby Ipswich, the first record appeared (Webber, 1968) for the occurrence of *V. compacta* (Collins) Collins var. *koksoakensis* Blum & Wilce in the United States. This taxon was described originally for the North American continent from Labrador by Blum & Wilce (1958).

Thus, field and laboratory studies of *Vaucheria* species, as they occur in the extensive salt marshes of New England, continue to be fruitful areas of investigation for the marine botanist.

Within the past few months, this statement was reaffirmed with particular interest. In July, 1973, I visited a

[1]Contribution No. 28 from the Marine Science Institute, Nahant, Mass. The author appreciates the comments of Dr. J. L. Blum in a preliminary reading of this manuscript.

marsh adjacent to Jones Creek along the Annisquam River, Gloucester, collecting especially for marine Cyanophyta and *Vaucheria.*[2] Samples of the latter were taken from beneath a very dense cover of *Spartina patens* in the upper littoral portion of the marsh. In early September, 1973, I made additional collections of *Vaucheria* mats, this time at a marsh at the intersection of Crafts Rd. and State Rt. 128, Gloucester. The plants here formed a distinct line of growth at the *Spartina alterniflora-Spartina patens* interface, inhabiting not only the mud, but frequently growing upon the previous year's leaves and culms of *S. alterniflora.* Samples from both sites were maintained temporarily in dim light of a cold room (16°C.) at the Marine Science Institute.

On September 13, the *Vaucheria* plants, still vegetative, were returned to Keuka College for culturing. The conditions under which these samples were grown were: Erd-Schreiber medium (Provasoli, et al., 1957), a 14/10 LD cycle at approximately 75-100 f.c., and a temperature of 15°C. Under these conditions, reproductive structures were apparent within a month, and species identification was possible.

The plants from both sites in Gloucester were readily recognizable as *Vaucheria nasuta* Taylor & Bernatowicz, described originally from Bermuda (Taylor & Bernatowicz, 1952). A few years later, Bernatowicz (1958) published what appears to be the first account of this species in the United States. He located *V. nasuta* at the Barnstable Marsh (Cape Cod) in Massachusetts, finding it "sparingly reproductive" in the field during August. Ott (personal communication) has determined this species from North Carolina, and Blum (1971) has since recorded it from a California salt marsh. Thus, to date, the known world distribution of *Vaucheria nasuta* is from four somewhat disjunct localities: Bermuda, North Carolina, Massachusetts and California.

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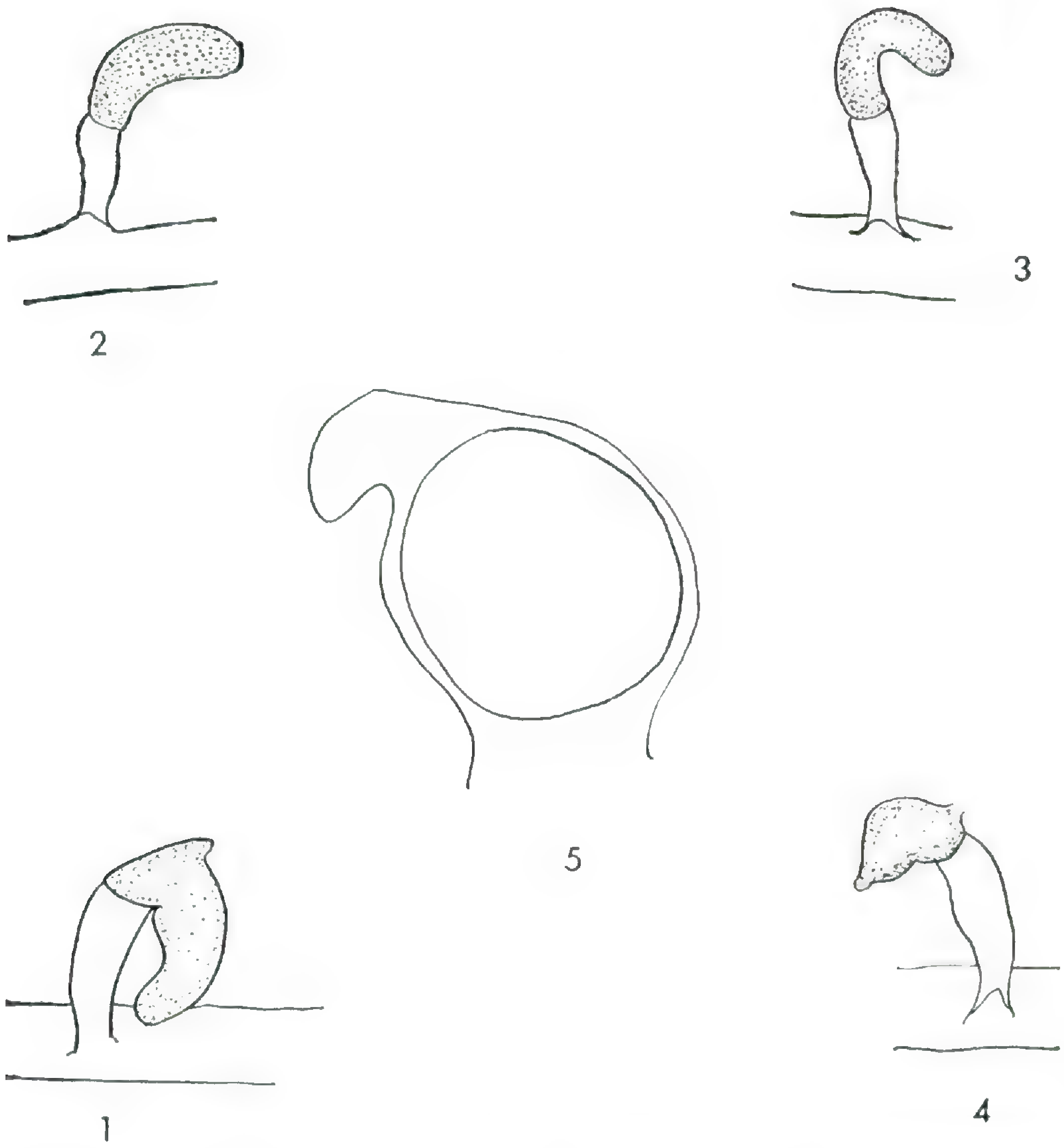
[2]Supported by a grant from the American Philosophical Society.



Figures 1-5. *Vaucheria nasuta*, cultured material, from Gloucester. All figs. ×430.

Although somewhat larger in dimensions, the Gloucester plants agree generally with those measurements reported for the original Bermudian material. Filament diameters, both from field collections and from cultured plants, were (32μm) 43μm-51μm (60μm). *Vaucheria nasuta* is monoecious; the antheridia were usually scattered along the length of the filaments, and not immediately adjacent to the oogonia. In a few instances, however, they were clustered about an oogonium, essentially in the manner shown by Blum (1972, p. 41, Figs. 86-87). The male gametangia

consistently tapered to the base, were expanded slightly above, and measured 20-38μm in width. At maturity, each antheridium curved markedly toward the filament, not infrequently assuming a circular configuration (Fig. 1). Each antheridium is subtended by a hyaline basal cell which is cut off just after this young reproductive structure begins its bending posture (Figs. 2, 3). I observed one such basal cell which was divided as shown by Taylor & Bernatowicz (1952, *Pl.* II, Fig. 13). Discharge of antherozoids is effected either by a single terminal pore, or, more commonly, by one lateral and one terminal pore (Fig. 4). These pores are often slightly tubular. The oogonia (to 175μm long) are markedly beaked, and tend to be appressed toward the filament. The somewhat spherical oospores (150μm-200μm) almost fill the oogonia (Fig. 5).

LITERATURE CITED

BERNATOWICZ, A. J. 1958. A Bermudian marine *Vaucheria* at Cape Cod. Biol. Bull. **151**(2):344.

BLUM, J. L. 1960. A new *Vaucheria* from New England. Trans. Amer. Microscop. Soc. **79**(3):298-301.

————. 1971. Notes on American Vaucheriae. Bull. Tor. Bot. Club **98**:189-194.

————. 1972. Vaucheriaceae. N. Am. Flora. II. 8:1-64.

————, & J. T. CONOVER. 1953. New or noteworthy Vaucheriae from New England salt marshes. Biol. Bull. **105**(3):395-401.

————, & R. T. WILCE. 1958. Description, distribution and ecology of three species of *Vaucheria* previously unknown from North America. Rhodora **60**:283-288.

PROVASOLI, L., J. MCLAUGHLIN, & M. DROOP. 1957. The development of artificial media for marine algae. Archiv. Microbiol. **25**:392-428.

TAYLOR, W. R., & A. J. BERNATOWICZ. 1952. Marine species of *Vaucheria* at Bermuda. Bull. Mar. Sci. Gulf Carib. **2**(2):405-413.

WEBBER, E. E. 1968. New England salt marsh Vaucheriae. Rhodora **70**:274-277.

————, & R. T. WILCE. 1971. Benthic salt marsh algae at Ipswich, Massachusetts. Rhodora **73**:262-291.

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RANUNCULUS CYMBALARIA PURSH VAR. ALPINUS HOOK.

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Ranunculus cymbalaria Pursh var. *alpinus* Hook. was described in 1829 by Sir Wm. J. Hooker from a specimen "found by Mr. Drummond upon the Rocky Mountains" (Hooker, 1829, p. 12). It was distinguished by its small size, three-toothed leaf apices, and single-flowered scapes. Hooker felt that this variety was so close to *R. halophilus* Schlecht. that he reduced Schlechtendal's species to synonymy under var. *alpinus*. The validity of this variety has been under discussion since the early part of this century. Fernald (1914, p. 162) suggested that this variety "seems to be merely a dwarfed extreme such as can be found in unfavourable habitats nearly throughout the range." This doubt as to the validity of the variety was also emphasized by Benson (1948, p. 216). He said that "the status of the variety is not wholly beyond question, since leaves of var. *alpina* [*alpinus*][1] type develop at the beginning of growth at each of the nodes of the stolons of the intermediate forms between var. *typicus* [*cymbalaria*][1] and var. *alpina* [*alpinus*]."[1] He also suggested that "transplant experiments would be significant." Variety *alpinus* was reported by Benson (1948) from Alaska to Newfoundland in North America and var. *cymbalaria* was reported from a similar range and farther south.

Living specimens of var. *alpinus* were collected from brackish estuaries at Main Brook on the Northern Peninsula and Stephenville Crossing in Newfoundland. All of the leaves of these specimens were small (average 7 mm long by 6 mm broad) and the petals were about 2.5 mm long. They were grown under the same environmental conditions in the greenhouse at the University of Alberta, Canada, with collections of *Ranunculus cymbalaria* var. *cymbalaria* from Alberta. All of the plants were washed free of soil after collection in the field, potted, and grown

[1]Benson, 1954. p. 363.

under the same conditions of soil (2 loam: 1 peat: 1 sand), light (daylight), temperature (20°C day, 17°C night), and humidity (not controlled). The Newfoundland collections grew as large or larger than the Alberta collections in all respects. The leaves were an average of 18 mm long by 14 mm broad and the flowers were of the same size as var. *cymbalaria* (petals about 4.5 mm long). Average measurements of Albertan var. *cymbalaria* in the greenhouse were: leaves — 17 mm long by 15 mm broad and petals — 4.2 mm long. In the field, the leaves of the Newfoundland specimens were typical of var. *alpinus*. They were only three-toothed at the apex and truncate at the base. After about a year's growth in the greenhouse, these specimens produced leaves that were crenate to the decidedly cordate base, and they were much larger in overall size. There was no indication of reversion to the characters they had under field conditions.

It is, therefore, proposed that *Ranunculus cymbalaria* Pursh var. *alpinus* Hook. be considered a synonym of *R. cymbalaria* Pursh.

Collections used in this study: NEWFOUNDLAND: Main Brook, Northern Peninsula, *Maunder*, Aug. 8, 1971 (ALTA); Stephenville Crossing, *Scott* 1797 (ALTA). ALBERTA: Medicine Hat, *Scott* 1269 (ALTA); Long Lake, *Scott* 1676 (ALTA); Nordegg, *Scott* 1480 (ALTA); Twin Butte, *Scott* 1417 (ALTA); Marwayne, *Scott* 1714 (ALTA); Cold Lake, *Dumais* 5456 (ALTA). Three plants were collected at each site.

LITERATURE CITED

BENSON, L. 1948. A treatise on the North American Ranunculi. Amer. Midl. Nat. **40**: 1-261.

————. 1954. Supplement to a treatise on the North American Ranunculi. Amer. Midl. Nat. **52**: 328-369.

FERNALD, M. L. 1914. The variations of *Ranunculus cymbalaria*. Rhodora **16**: 160-163.

HOOKER, W. J. 1840. Flora Boreali-Americana. H. G. Bohn. London. 2 vols. plus Atlas volume with 238 plates.

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SYSTEMATICS OF PALAFOXIA (ASTERACEAE:HELENIEAE)[1]

B. L. TURNER AND MICHAEL I. MORRIS[2]

The genus *Palafoxia* was proposed by Lagasca (1816) who applied the generotype to a plant originally collected in "New Spain" and which Cavanilles (1794) had at first termed *Ageratum lineare* and later (1797) *Stevia linearis*. Cassini (1818) placed *Palafoxia linearis* in synonymy under his own *Paleolaria carnea* which cannot be recognized since Lagasca's earlier name has priority.

Since Cassini's work, *Palafoxia* has been split into as many as three genera, although Bentham and Hooker (1873), Hoffmann (1894), Cory (1946), and Shinners (1949) recognized only the single genus. *Polypteris* was proposed by Nuttall (1818) and subsequently sanctioned by Gray (1884), Bush (1904), Rydberg (1914) and Baltzer (1944), the last three of whom also sustained Rafinesque's (1836) segregate genus, *Othake*.

In our opinion, *Polypteris* and *Othake* cannot be retained apart from *Palafoxia* because they are too inextricably bound as a phyletic group to be treated as segregate genera. To place emphasis on putative diagnostic characters such as comparative length of corolla parts and phyllary texture, as was done by the several authors men-

[1]Supported, in part, by National Science Foundation Grant 29576X.

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tioned, appears biologically unsound because it stresses cryptic differences and ignores the presence of an overwhelming multitude of morphological and cytological similarities which collectively suggest that the three taxa belong within the confines of a single generic unit.

In the present account, *Palafoxia* is treated as composed of 12 species (and 6 varieties), 9 annuals and 3 perennials, occurring mostly in sandy soils of southwestern United States and Mexico, although *P. feayi* and *P. integrifolia* are indigenous to Florida. While most of the taxa are locally very common and widespread, six are rare and/or endemic: *P. reverchonii, P. hookeriana, P. arida* var. *gigantea, P. riograndensis, P. texana* var. *robusta,* and *P. lindenii.*

GENERIC POSITION

Palafoxia has been classically treated as a member of the tribe Helenieae and the sole representative of the subtribe Palafoxianae. The phyletic affinities of *Palafoxia* to other genera in the Helenieae are controversial (Turner and Powell, 1977). Most workers recognize *Palafoxia* as distinct from, but closely related to, *Bahia, Florestina, Hymenothrix,* and *Schkuhria,* all members of the subtribe Bahiinae. Turner's (1963) hypothetical diagram, illustrating the relative relationships of these 5 helenioid genera, suggests that *Florestina* is the most closely allied member of the Bahiinae to *Palafoxia.* However, we disagree with Shinners' (1949, 1952) expanded concept of *Palafoxia* which includes *Florestina.* Although the two genera are quite similar with respect to habit and inflorescence type, they differ markedly in certain floral structures. The disc corollas of *Palafoxia* are regular, but irregular in *Florestina;* the style branches of *Palafoxia* are linear, revolute, and hispidulous whereas those in *Florestina* are flattened with cuspidate appendages and tend to be glabrous.

In spite of the seemingly close relationship of *Palafoxia* to *Florestina,* Turner and Powell (1977) reckon *Palafoxia* to be sufficiently remote to be included, along with *Marshallia,* as members of the subtribe Palafoxianae and positioned in the tribe Eupatorieae.

FLAVONOID CHEMISTRY

Intra- and inter-populational samples of selected species of *Palafoxia* were analyzed for flavonoid content. Dried leaves and stems of these samples were finely ground in a Waring Blender and extracted at room temperature in cold 85% methanol (aq.) for 24 hours. The resultant crude extract was subsequently concentrated, spotted on Whatman 3MM chromatography paper, and developed two-dimensionally in tertiary butyl alcohol (TBA) and acetic acid (HOAc) solvent systems.

All of the flavonoid spots from each of the plant samples were found to be purple under UV light, but extremely faint suggesting very low compound concentration. Furthermore, the color of each spot changed to yellow-green when subjected to ammonia and viewed under UV light. With respect to spot color and also R_f values, each of the observed flavonoids could be classified as being either flavonol monoglycosides or diglycosides with hydroxyl functions at both the 4′ and 5 positions.

CHROMOSOME NUMBERS

Meiotic chromosome counts, available from 11 of 12 species and 4 of 6 varieties of *Palafoxia,* were found to be $n = 10$, 11, and 12 (Table 1). Both meiotic and mitotic material were stained with acetocarmine and all configurations were quite clear. At diakinesis and metaphase I, bivalents with two chiasmata were normally formed while mitotic figures showed large well-differentiated chromosomes (Figs. 1-2). All of the 86 collections examined were found to be diploid.

Table 1. Collections of *Palafoxia* examined for chromosome number.

Species	Locality and voucher*	n = number
P. arida var. *arida*	Ariz. MOHAVE CO.: *T.* 4787.	12
	Ariz. YUMA CO.: *T.* 4756.	12
	Calif. IMPERIAL CO.: *T.* 4758.	12
	Calif. RIVERSIDE CO.: *P. & S.* 1383.	12
	Calif. IMPERIAL CO.: *R.* 11506A.	12
	Mex. BAJA CALIF. *S & B.* 298.	12
	Mex. BAJA CALIF. *P. & T.* 1705.	12
	Mex. BAJA CALIF. *P. & T.* 1730.	12
	Mex. BAJA CALIF. *P. & T.* 1818.	12
	Mex. SONORA. *R.* 11677A	12
	Mex. SONORA. *S. & B.* 167a.	12
P. arida var. *gigantea*	Calif. IMPERIAL CO.: *R.* 12910A.	12
	Calif. IMPERIAL CO.: *T.* 4757.	12
	Calif. IMPERIAL CO.: *T.* 4759.	12
P. callosa	Tex. BANDERA CO.: *T.* 3840.	10
	Tex. FAYETTE CO.: *T.* 4452.	10
	Tex. KENDALL CO.: *T.* 3834.	10
	Tex. LAMPASAS CO.: *T.* 4587.	10
	Tex. LLANO CO.: *T.* 3483.	10
	Tex. MC CULLOCH CO.: *Smith* 232 (KANU)B	10
	Tex. VAL VERDE CO.: *T.* 3252	10
	Tex. VAL VERDE CO.: *T.* s.n.	10
	Tex. COLEMAN CO.: *T.* 4860.	10
	Mex. COAHUILA: *P. et al.* 1587	10
	Mex. COAHUILA: *P. et al.* 1411C.	10
P. feayi	Fla. LAKE CO.: *T.* 4663.	12
	Fla. COLLIER CO.: *Plettman & T.* F-15	12
P. hookeriana var. *hookeriana*	Tex. BASTROP CO.: *Smith* 555 (KANU)B (reported as *P. sphacelata*)	12
	Tex. LAVACA CO.: *T.* 3273.	12
	Tex. LIBERTY CO.: *T.* 4617.	12
	Tex. WASHINGTON CO.: *T.* 3917.	12
P. hookeriana var. *minor*	Tex. FREESTONE CO.: *T.* 4449.	12
	Tex. FREESTONE CO.: *T.* 4443.	12
	Tex. LEON CO.: *T.* 4429.	12
Palafoxia integrifolia	Fla. LEON CO.: *T.* 4657.	12
Palafoxia lindenii	Mex. VERACRUZ: *King* 2418.	11

Table 1 (continued)

Species	Locality and voucher*	n = number
Palafoxia reverchonii	**Tex.** ANDERSON CO.: *T.* 5743.	12
	Tex. HENDERSON CO.: *T.* 5742.	12
	Tex. HOUSTON CO.: *T.* 5746.	12
	Tex. UPSHUR CO.: *King* 2182.	12
Palafoxia riograndensis	**Mex.** COAHUILA: *Flyr* 247.	12
Palafoxia rosea var. *macrolepis*	**N. Mex.** ROOSEVELT CO.: *T.* 4720.	10
	Tex. ANDREWS CO.: *Melchert* 228.	10
	Tex. ANDREWS CO.: *Melchert* 225.	10
	Tex. COCHRAN CO.: *T.* 4718.	10
	Tex. FAYETTE CO.: *Smith* 552 (KANU)[B] (reported as *P. integrifolia*)	10
	Tex. LIVE OAK CO.: *Thompson & T.* 12.	10
	Tex. LLANO CO.: *T.* 2512.	10
	Tex. MEDINA CO.: *Johnston et al.* 3438.	10
	Tex. MOTLEY CO.: *Tomb* 148.	10
	Tex. WILSON CO.: *T.* 4423.	10
	Tex. WILSON CO.: *Sullivan & T.* 1.	10
Palafoxia rosea var. *rosea*	**Tex.** FREESTONE CO.: *T.* 4447.	10
	Tex. GALVESTON CO.: *T.* 3070.	10
	Tex. LEON CO.: *T.* 4437.	10
Palafoxia sphacelata	**Mex.** CHIHUAHUA: *Stuessy* 1115.	12
	N. Mex. DE BACA CO.: *T.* 5672.	12
	N. Mex. LEA CO.: *T.* 2945. (SMU)	12
	Okla. WOODS CO.: *Tomb* 593.	12
	Tex. CRANE CO.: AVERETT 213, 214[C].	12
	Tex. PECOS CO.: *Watson* 142	12
	Tex. WARD CO.: *Melchert* 251.	12
Palafoxia texana var. *ambigua*	**Tex.** ARANSAS CO.: *T.* 5035.	11
	Tex. HIDALGO CO.: *T.* 4481.	11
	Tex. KARNES CO.: *T.* 5017.	11
	Tex. NUECES CO.: *T.* 3961.	11
Palafoxia texana var. *texana*	**Mex.** COAHUILA: *Flyr* 236, 237.	11
	Mex. COAHUILA: *P.* 501, 503, 519.	11
	Mex. COAHUILA: *Rock* M-488.	11
	Mex. COAHUILA: *T.* 2981, 6007.	11
	Mex. NUEVO LEON: *McGregor* 16752 (KANU).	11
	Mex. TAMAULIPAS: *King* 2209.	11

Table 1 (continued)

Species	Locality and voucher*	$n =$ number
Palafoxia texana var. *texana*	Tex. ATASCOSA CO.: *T.* 4982.	11
	Tex. FRIO CO.: *Sullivan & T.* 15.	11
	Tex. FRIO CO.: *Sullivan & T.* 18.	11
	Tex. FRIO CO.: *T.* 4558.	11
	Tex. HIDALGO CO.: *T.* 4481.	11
	Tex. HIDALGO CO.: *Strother* 82.	11
	Tex. MEDINA CO.: *T.* 4561.	11
	Tex. MC MULLEN CO.: *Flyr* 168.	11
	Tex. STARR CO.: *T.* 4512.	11
	Tex. STARR CO.: *T.* 4501.	11
	Tex. VAL VERDE CO.: *Melchert* 263.	11
	Tex. VAL VERDE CO.: *P. & Watson* 1399[C].	11
	Tex. WEBB CO.: *Melchert* 272.	11
	Tex. ZAVALA CO.: *T.* 5001.	11

*Except where spelled out, collectors are abbreviated as follows: *B* for Babcock; *P* for Powell; *R* for Raven; *S* for Sikes; *T* for Turner. Unless specified, voucher specimens are deposited in TEX.

[A]Raven, P. H. and D. W. Kyhos, *In:* Am. J. Bot. **48**:842-850. 1961.

[B]Smith, E. B. and R. R. Johnson, *In:* Madrono **17**:268. 1964.

[C]Powell, A. M. and S. Sikes, *In:* Southwest. Naturalist **15**:175-186. 1970.

Except in synthetic interspecific hybrids between *P. rosea* ($n = 10$) and *P. callosa* ($n = 10$), meiosis was nearly always regular and fragments were only infrequently observed. Meiotic figures from F_1 hybrids between the single synthetic cross attempted showed bridges and fragments in about 50% of the cells examined; the remaining 50% appeared normal.

Fig. 1. Meiotic chromosomes of *Palafoxia rosea* var. *rosea* ($n = 10$); ×3400.

Fig. 2. Mitotic chromosomes of *Palafoxia rosea* var. *rosea* ($2n = 20$); $\times 3400$.

GENERIC ORIGIN

Although phylogenetic histories of a genus are necessarily hypothetical, certain geobotanical considerations correlated with cytological data provide interesting clues to the origin of *Palafoxia* and attendant species. The ancestral prototype of *Palafoxia* probably originated in tropical America from Eupatorioid stock or derivations thereof. According to Shinners (1952), *Palafoxia* evolved during the Miocene as an autochthonous element of the Texas-North Mexican (Mexican Plateau) flora which migrated northeastward to the Edwards Plateau and Trans-Pecos regions of present-day Texas. If Shinners is correct, it is very possible that the genus became initially established within an area now generally known as south-central Texas from where the incipient stages of evolutionary divergence occurred.

We view the origin of the group somewhat differently. It is surmised that the rayed species of *Palafoxia*, *P. reverchonii*, *P. sphacelata*, and *P. hookeriana*, each possessing the base chromosome number, $x = 12$, represent the most primitive members of the genus and constitute a closely related monophyletic unit from which the remaining nine eradiate species ultimately had their origin. This being so, we visualize the primitive species as being relictual elements of a neotropical flora which occupied much of the southeastern United States during the early Terti-

ary. The peripheral, more advanced taxa such as *Palafoxia texana* ($n = 11$), *P. lindenii* ($n = 11$), *P. rosea* ($n = 10$), and *P. callosa* ($n = 10$) were evidently derived by progressive aneuploid reduction from the ancestral base of $x = 12$, the first 3 species adapting to sandy soils, *P. callosa* to limestone soils. *Palafoxia lindenii,* an endemic to the sand dunes of Veracruz, Mexico and vicinity, is very closely related to *P. texana* and is, presumably, a recent insular-type derivative from the latter species. Insular adaptation of divergent *Palafoxia* populations to sand dune habitats is not an uncommon phenomenon and has probably occurred independently in the genus several times. With respect to *P. linearis, P. arida, P. riograndensis, P. feayi,* and *P. integrifolia,* populations representing their differentiating gene pools could have been subjected to disruptive selection pressures which eventually led these evolving groups to occupy ecologically similar (sandy), but spatially disjunct habitats.

Table 2. Selected characteristics of *Palafoxia* listed according to their adjudged primitive and advanced states.

Primitive Characters	Advanced Characters
Heads rayed	Heads eradiate
$n = 12$	$n = 11, 10$*
Annual	Perennial
Outer disc florets regular	Outer disc florets irregular
Leaves petioled	Leaves sessile
Lobes of disc corollas longer than throat	Lobes of disc corollas shorter than throat
Phyllaries tending to be broadened: ovate, obovate, lanceolate	Phyllaries tending to be narrowed: oblong, elliptic, linear
Pappus of outer disc florets monomorphic	Pappus of outer disc florets dimorphic
Phyllaries green, foliaceous	Phyllaries white, membranous

*Highly advanced

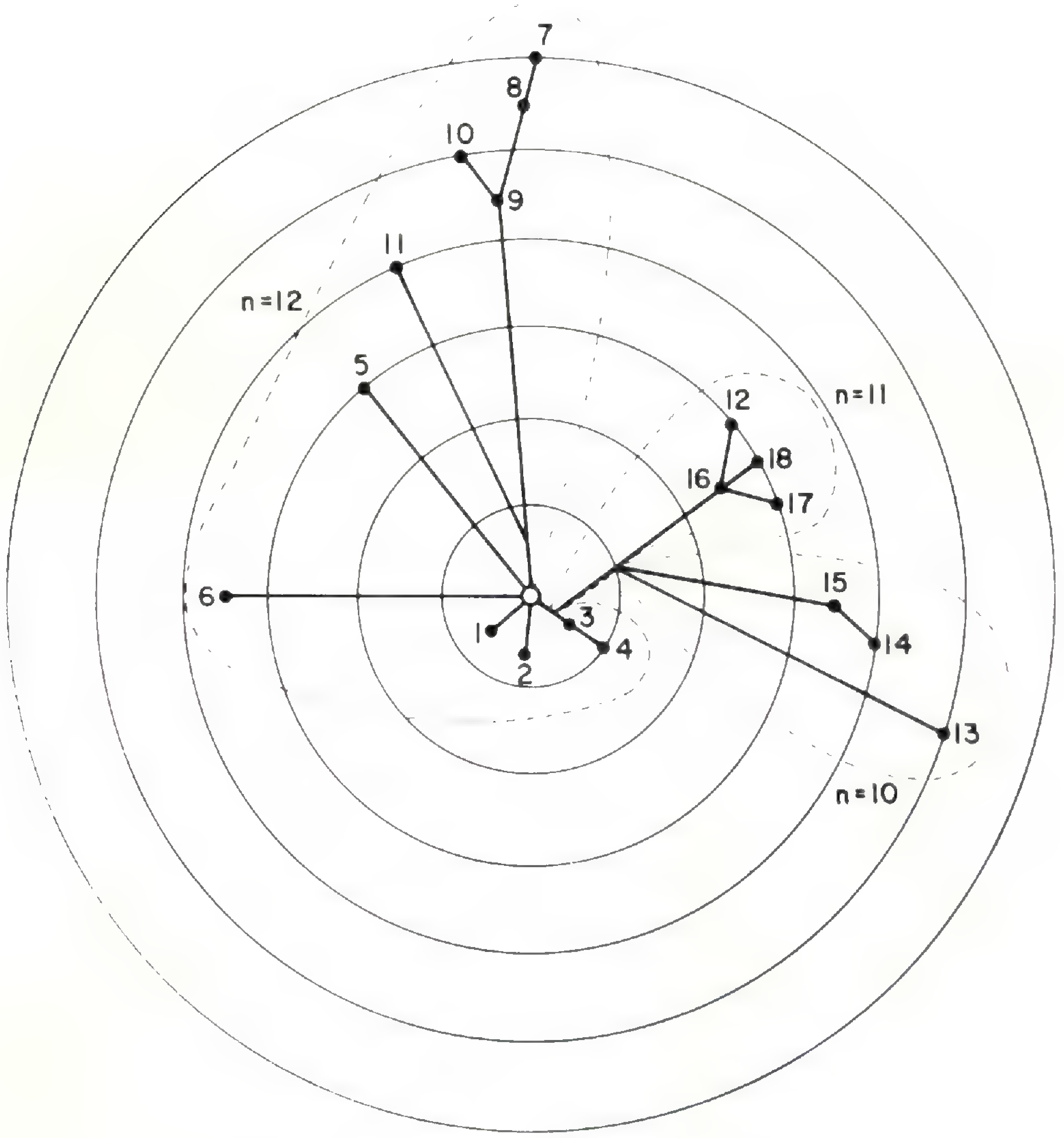

Fig. 3. Hypothetical phylogenetic diagram showing the species and varieties of *Palafoxia* as indicated by number: (1) *reverchonii;* (2) *sphacelata;* (3) *hookeriana* var. *hookeriana;* (4) *hookeriana* var. *minor;* (5) *feayi;* (6) *integrifolia;* (7) *linearis* var. *linearis;* (8) *linearis* var. *glandulosa;* (9) *arida* var. *arida;* (10) *arida* var. *gigantea;* (11) *riograndensis;* (12) *lindenii;* (13) *callosa;* (14) *rosea* var. *rosea;* (15) *rosea* var. *macrolepis;* (16) *texana* var. *texana;* (17) *texana* var. *ambigua;* (18) *texana* var. *robusta.* The common ancestor is represented by the origin and each consecutive, concentric level symbolizes an incremental advancement of 1.0 (e.g., outermost circle = 6.0).

Table 2 lists certain characteristics according to their adjudged states of primitiveness and advancement. "Generalized" characters were not necessarily considered to be primitive. Numerical values of 0 and 1 were assigned to characters deemed primitive and advanced, respectively. Highly advanced characters were assigned a value of 2. Each species and variety was arranged according to its hypothetical phylogenetic relationships (Fig. 3).

TAXONOMY

PALAFOXIA Lagasca

Palafoxia Lagasca, Elench. Pl. Hort. Matr. 26. 1816; Gen. et Sp. Nov. 26. 1816.

Paleolaria Cassini, Bull. Soc. Philom. 198. 1816; Dict. Sci. Nat. 1, Suppl. 59. 1816.

Polypteris Nuttall, Gen. N. Am. Pl. 2: 139. 1818.

Lomaxeta Rafinesque, New Fl. Am. 4: 72. 1836.

Othake Rafinesque, New Fl. Am. 4: 73. 1836.

Taprooted annuals or perennials; stems erect or ascending, brittle-herbaceous, suffruticose to woody in certain species, variously branched to nearly simple, densely glandular-pubescent to almost glabrous; leaves alternate (usually opposite at first), firm-membranous, petiolate (rarely sessile); blades linear to broadly lanceolate, entire; heads irregularly corymbiform at the top of the plant, 3-28 mm high; involucre cylindric to broadly turbinate; receptacle flat, naked; phyllaries 2-3 seriate, subequal, linear to obovate, green, thickish to membranous, the margins often tinged red-purple, pubescence when present commonly interspersed with glandular trichomes; ray flowers absent or present, when present pale to dark violet, prominently 3-toothed terminally, pistillate, fertile; disk flowers white to violet, perfect, fertile, corollas regular or irregular, 5-lobed terminally; style branches linear, spreading or revolute, hispidulous; achenes 4-angled, obpyramidal; pappus

of 4-10 scales, varying from a minute callosity to a long acuminate hyaline-margined callose midrib, prominently dimorphic in certain species; gametic chromosome numbers, $n = 10$, 11, 12. Type species: *Palafoxia linearis* (Cav.) Lagasca.

KEY TO SPECIES AND VARIETIES OF PALAFOXIA

A. Heads with conspicuous rays . . . . B.
- B. Leaves linear, narrowly lanceolate, 2-4(-6) mm wide; stems not glandular except for inflorescence; achenes 5-6 mm long; involucral bracts 6-7(-8) mm long . . . . 1. *P. reverchonii*
- B. Leaves lanceolate to ovate-lanceolate, 3-20 mm wide; stems usually glandular for some distance below inflorescence, often conspicuously so; achenes 6-9 mm long; involucral bracts 7-20(-25) mm long . . C.
  - C. Heads narrowly turbinate to cylindric; involucral bracts 2.0-2.5(-3) mm wide; ligule of ray mostly 10 mm long or less; stems not robust, branching at or below middle (except in immature or depauperate specimens); species of western Texas, New Mexico, and adjacent Mexico . . . . 2. *P. sphacelata*
  - C. Heads broadly turbinate to campanulate; involucral bracts 2-5 mm wide; ligule of ray mostly 10 mm long or more; stems robust, branched at or above middle (except in mowed or injured specimens); species of eastern Texas . . . . . D.
    - D. Stems densely glandular-pubescent throughout; involucre, in flower, 10-16 mm high; florets 50-90 per head . . . . 3a. *P. hookeriana* var. *hookeriana*
    - D. Stems glandular-pubescent only in the upper portions; involucre, in flower, 7-12 mm high; florets 25-50 per head . . . . 3b. *P. hookeriana* var. *minor*

A. Heads without rays (peripheral florets inconspicuously zygomorphic in *P. riograndensis*) . . . . E.

E. Species of southeastern U. S. (principally Florida) . . . . F.

F. Involucral bracts linear, herbaceous, green; spindly shrubs 1-3 m tall . . . . . 4. *P. feayi*

F. Involucral bracts narrowly elliptic to obovate, membranous, white; perennial herbs 0.3-1.0 m tall . . . . 5. *P. integrifolia*

E. Species of southwestern U. S. (west of Mississippi River) and Mexico . . . . G.

G. Corolla lobes short, about 1/5 as long as the elongate throat; species of Sonoran and Mojave deserts (southwestern-most Utah to southern-most Baja California, Mexico) . . . . H.

H. Leaves linear, obtuse or rounded at apex; sprawling shrublets of southern Baja California (occasional adventive in dune sand along beaches of Sonora, Mexico) . . . . . I.

I. Mid-stem foliage (and most others) rather evenly pubescent with appressed white hairs and without glandular trichomes . . . 6a. *P. linearis* var. *linearis*

I. Mid-stem foliage (and most others) densely covered with a rough glandular pubescence . . . . 6b. *P. linearis* var. *glandulosa*

H. Leaves linear-lanceolate, acute at apex; strictly erect, taprooted annuals of more northern distribution . . . . J.

J. Plants not robust, 0.3-0.9 m tall, the primary stem 0.5 cm thick or less; heads (including disc florets), 20-25(-28) mm long; widespread in the Sonoran desert . . . . 7a. *P. arida* var. *arida*

J. Plants robust, 0.9-1.5 m tall, the primary stem 0.5-1.0 cm thick; heads 28-35 mm long; endemic to large sand dunes west

of Yuma, Arizona ....
.... 7b. *P. arida* var. *gigantea*

G. Corolla lobes longer than throat; species of the Chihuahuan desert, Mexico, and eastward .. K.

K. Involucre cylindric; corolla of outermost florets zygomorphic; achenes (7-)8-11 mm long .... 8. *P. riograndensis*

K. Involucre turbinate; corollas regular; achenes 4-7 mm long .... L.

L. Leaf blades greyish puberulent, widest at or near the middle; achenes glabrous or nearly so .... 9. *P. lindenii*

L. Leaf blades greenish, often whitish canescent; achenes pubescent .... M.

M. Leaves mostly linear to narrowly lanceolate, 2-6 mm wide; chromosome number, $n = 10$; species of southcentral to western Texas and northward .... N.

N. Involucral bracts narrowly linear, 0.6-1.3 mm wide; pappus 0.5-2.0 mm long; species on predominantly limestone soils .... 10. *P. callosa*

N. Involucral bracts linear to obovate, mostly 1.2-2.5 mm wide; pappus 1.0-8.0 mm long; species on predominantly sandy soils .... O.

O. Pappus scales mostly short, obtuse to acute, 1.0-3.0 mm long; involucral bracts 5-7 mm long; plants of southcentral Oklahoma and eastern Texas .... 11a. *P. rosea* var. *rosea*

O. Pappus scales mostly long, acute to long acuminate, 3.0-8.0 mm long; involucral bracts 7-10 mm long .... 11b. *P. rosea* var. *macrolepis*

M. Leaves mostly broad lanceolate, 6-15 mm wide; chromosome number, $n = 11$, species of southcentral Texas and southward .... P.

P. Pappus scales of inner achenes 3-5(-6) mm long; involucral bracts broadly linear to oblanceolate, pubescence interspersed with glandular trichomes; main stem usually branched below; usually occur-

ring in rocky limestone soils . . . . 12a. *P. texana* var. *texana*

P. Pappus scales of inner achenes 1-3(-4) mm long; involucral bracts linear, usually lacking glandular trichomes; main stem usually unbranched below (except following injury); usually occurring in silty alluvial or sandy soils . . . . Q.

Q. Achenes 4.0-5.5 mm long; plants of southernmost Texas and adjacent Mexico . . . . 12b. *P. texana* var. *ambigua*

Q. Achenes 6-7 mm long; plants of coastal sand dunes of central Tamaulipas, Mexico . . . . 12c. *P. texana* var. *robusta*

Fig. 4. *Palafoxia reverchonii.* A. Whole plant, ×¼. B. Ray floret, ×3. C. Disc floret, ×3.

1. **Palafoxia reverchonii** (Bush) Cory, Rhodora 48:86. 1946. *Fig. 4*

Othake reverchonii Bush, Trans. Acad. Sci. St. Louis **14**: 180. 1904. TYPE: UNITED STATES. **Texas:** UPSHUR CO.: Big Sandy, *Reverchon* 3289 (Holotype, MO!; isotypes, NY!, 2 sheets). *Polypteris reverchonii* (Bush) Small, Fl. S.E. U. S. ed. 2, 1373. 1913.

Annual herbs 10-90 cm tall; stems brittle, dark green, rather evenly appressed pubescent throughout with short white hairs, without glandular trichomes except in the inflorescence; leaves opposite at first but soon alternate; mid-stem leaves narrowly lanceolate, 2-4(-6) mm wide, 30-90 mm long, petioles 3-10 mm long, blades appearing 1-nerved beneath, sparsely appressed hispid on both surfaces, the apices slender, acute; inflorescence an open corymb with 5-40 heads; heads turbinate 1.0-1.5 cm high, 15-35 flowered, on ultimate peduncles 1.5-8.0 cm long; principal involucral bracts 8-12, linear-lanceolate to somewhat obovate, 6-8 mm long, 1.5-3.0 mm wide, usually green and membranous along the margins, but occasionally purplish, pubescent with short, appressed hairs, these sparsely to densely interspersed with glandular trichomes; ray florets pale to dark violet, 15-25 mm long, the ligules with 3 linear lobes, these 4-5 mm long, 2-3 mm wide; disc corollas violet, regular, 5-8 mm long, the tube 3-5 mm long, abruptly flaring into a short throat 0.5-1.0 mm long, the lobes linear 2-3 mm long; achenes 5-6 mm long, uniformly short pubescent; pappus of disc florets composed of ca. 8 scarious, lanceolate, attenuate scales, 3-6 mm long, the mid-portion darker and somewhat indurate; ray pappus of 8 short, obovate scales ca. 0.5 mm long; chromosome number, $n = 12$.

Distribution: Sandy soils in upland pine and oak woodlands of eastern Texas. Flowering, Sept.-Oct. Fig. 5.

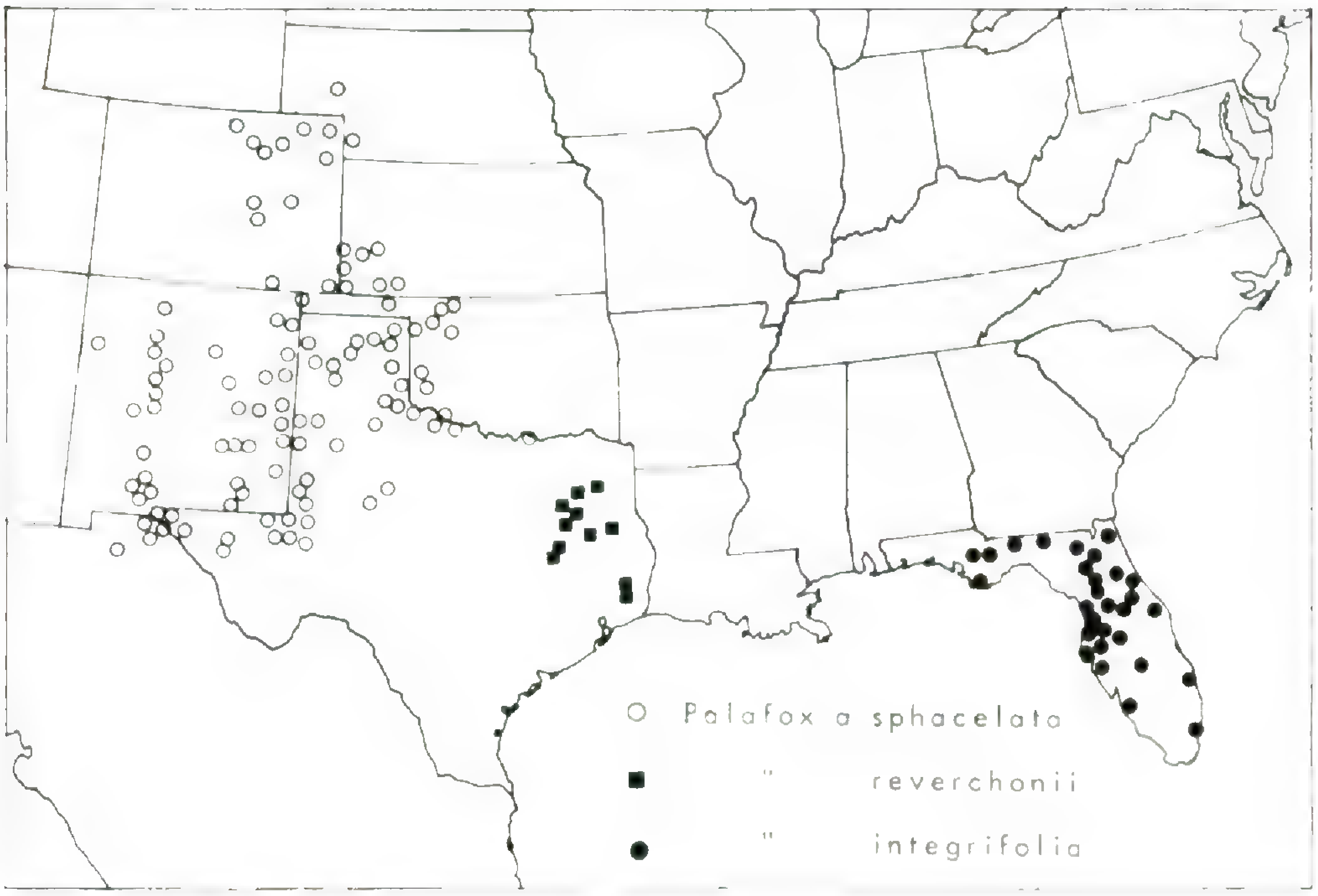

Fig. 5. Distribution of *Palafoxia sphacelata, P. reverchonii,* and *P. integrifolia.*

REPRESENTATIVE SPECIMENS: UNITED STATES. **Texas:** ANDERSON CO.: 6 miles NW Tennessee Colony, *Marsh, Jr.* 278 (TEX); Engeling area, *Marsh, Jr.* 56-43 (TEX); HARDIN CO.: 7.5 miles W of Silsbee, *Cory* 11327 (GH); HENDERSON CO.: Athens, *Turner* 5742 (TEX); HOUSTON CO.: Grapeland, *Palmer* 12834 (ARIZ, GH, NY, UC, US); LEON CO.: Centerville, *Fisher* (F); NACOGDOCHES CO.: Cushing, *Tharp & Brown* s.n. (TEX); UPSHUR CO.: 1.5 miles E of Big Sandy, *King* 2182 (SMU, TEX).

The species is most closely related to the allopatric *Palafoxia hookeriana* and might with some justification be treated as no more than a variety of that taxon. *Palafoxia reverchonii* is a much more delicate plant (with smaller heads, narrower leaves and fewer glands) than *P. hookeriana.* Through several years of field work, attempts at finding mixed populations of these two taxa were never successful. The taxa occur in seemingly pure populations near each other in Houston County, but were not found growing together.

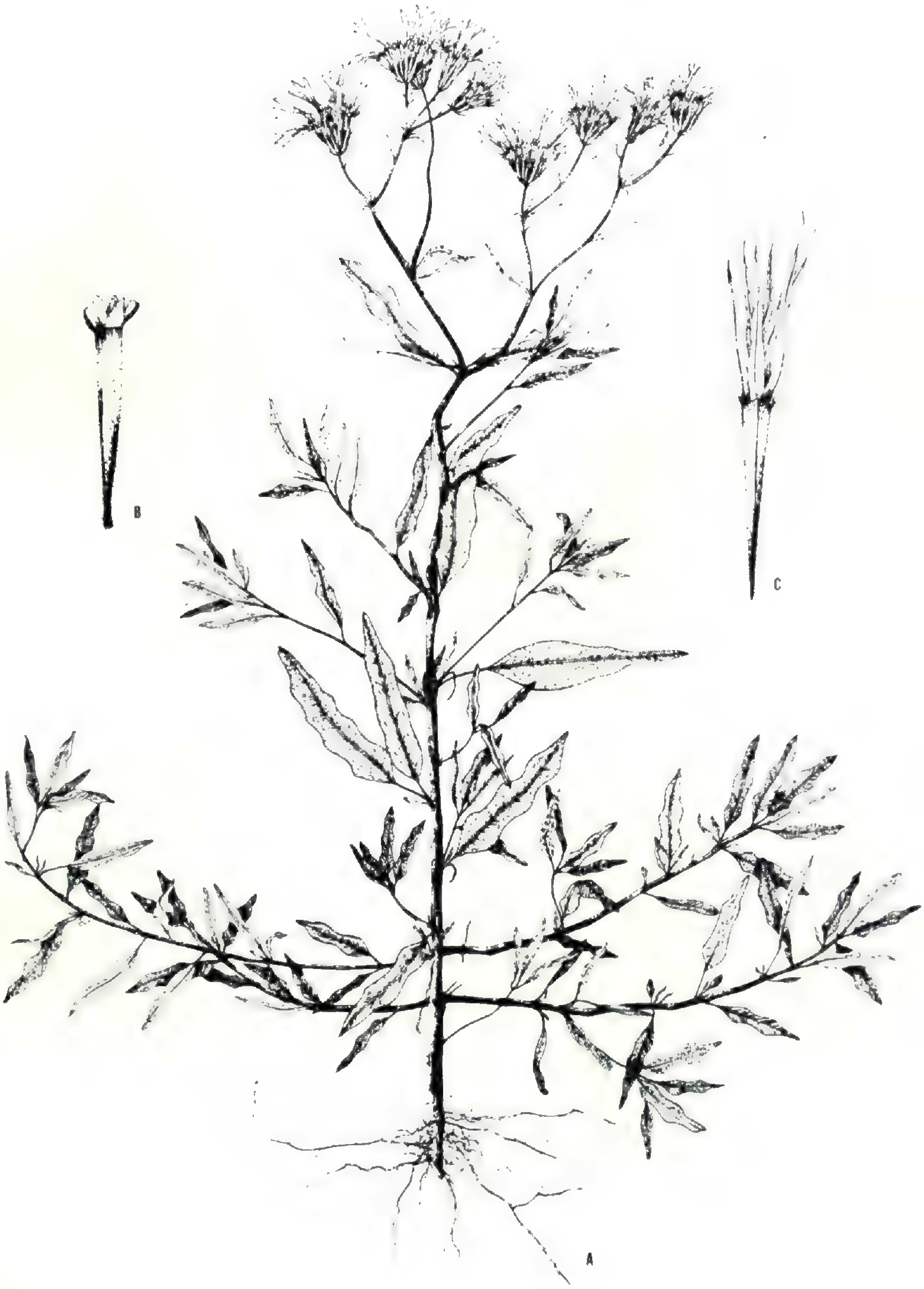

Fig. 6. *Palafoxia sphacelata.* A. Whole plant, ×¼. B. Ray achene and pappus, ×3. C. Disc achene and pappus, ×3.

2. **Palafoxia sphacelata** (Nutt. ex Torr.) Cory, Rhodora 48: 86. 1946. *Fig. 6.*

Stevia sphacelata Nutt. ex Torr., Ann. Lyc. N.Y. 2:214. 1828. TYPE: UNITED STATES. Without date or specific locality, probably in southeastern Colorado, *James,* (Holotype, NY!). *Palafoxia hookeriana* var. *subradiata* T. & G., Fl. N. Am. 2:368. 1842. *Polypteris sphacelata* (Nutt. ex Torr.) Trel. ex Branner & Cov., Ann. Rep. Geol. Surv. Arkansas 1888, 1:197. 1891. *Othake sphacelatum* (Nutt.) Rydb., Bull. Torr. Bot. Club 37:332. 1910. *Palafoxia hookeriana* Hook., *In:* Curtis's Bot. Mag. 91:t.5549. 1865. *non Palafoxia hookeriana* T. & G., 1842.

Annual herbs, 10-90 cm tall; stems brittle, becoming white and much-branched with age, merely hispid below, the upper portions densely glandular-pubescent; leaves simple, opposite at first but soon becoming alternate; mid-stem leaves broadly to narrowly lanceolate, even in the same population, 3-20 mm wide, 30-90 mm long, petioles 5-25 mm long, blades prominently 3-nerved beneath, roughly hispid on both surfaces, the apices acute; inflorescence corymbose with 3-20 heads; heads narrowly to broadly turbinate, 1-2 cm across, 1-2 cm high (including the exserted disc florets), 20-40 flowered, on ultimate peduncles 1.0-4.5 cm long; principal involucral bracts 10-12, linear-lanceolate, 9-12 mm long, 1.5-3.0 mm wide, usually purplish along the membranous margins, pubescent with short rough hairs, these interspersed with glandular-capitate trichomes; ray florets pale to dark violet, 15-25 mm long, the ligules with 3 narrow lobes 4-8 mm long, 1.5-3.0 mm wide; disc corollas pale violet, regular, 10-14 mm long, the tube 6-8 mm long, abruptly flaring into a short throat 1-2 mm long, the lobes linear, 3-5 mm long; achenes 6-9 mm long, uniformly short pubescent; pappus of disc florets composed of ca. 8 scarious, lanceolate, attenuate scales 7-9 mm long, the mid-portion darker and somewhat indurate; ray pappus of 8 short, obovate, erose scales, 0.2-0.7 mm long; chromosome number, $n = 12$.

Distribution: Mostly in sandy soils from northeastern Colorado south to trans-Pecos Texas and adjacent Mexico. Flowering, May-Nov. Fig. 5.

REPRESENTATIVE SPECIMENS. UNITED STATES. **Colorado:** BACA CO.: 4 miles N of Okla. line, *Rogers* 6418 (US); EL PASO CO.: between Drennen and Ellicott, *Bacigalupi* 858 (DS, GH, UC); LARIMER CO.: Ft. Collins, *Baker* 806 (MICH); LAS ANIMAS CO.: 3 miles SW of Tobe, *Rogers* 6128 (US); WELD CO.: Roggen, *Ramaley* 15136 (CAS, US); YUMA CO.: Wray, *Eggleston* 15535 (F). **Kansas:** MORTON CO.: S of Cimarron River, *Gates* 16175 (F); SEWARD CO.: Arkalon, *Kellerman* s.n. (US). **New Mexico:** BERNALILLO CO.: Isleta, *Arsene* 17503 (F, US); CHAVES CO.: 35 miles W of Roswell, *Earle & Earle* 381 (MO, US); DONA ANA CO.: Mesilla Valley, *Wooton* s.n. (ARIZ, DS, UC); EDDY CO.: Carlsbad, *Tracy* 8163 (F, GH, MO, US); GUADALUPE CO.: vicinity of Santa Rosa, *Arsene & Benedict* 16714 (F); MC KINLEY CO.: near Ft. Wingate, *Rusby* 211 (MICH); QUAY CO.: Nara Visa, *Fisher* 150 (US); ROOSEVELT CO.: 2.5 miles S of Tolar, *Tucker* 2959 (US); SANDOVAL CO.: Jemez Springs, *Nelson* 11680 (GH, MO, UC); SAN MIGUEL CO.: near Las Vegas, *Cockerell* (CAS); SIERRA CO.: near Elephant Butte Dam, *Archer* 408 (MICH); SOCORRO CO.: San Acacia, *O'Byrne & Magner* 3440-1 (MO); UNION CO.: 22 miles SW of Clayton, *Waterfall* 12283 (TEX); VALENCIA CO.: 8 miles S of Bellen, *Parker* 2408 (ARIZ, CAS). **Oklahoma:** BEAVER CO.: near Beaver, *Palmer* 41895 (MO, UC); BECKHAM CO.: SE part of county, *Eskew* 1524 (GH, MO, US); CIMARRON CO.: 1 mile W & 4 miles S of Kenton, *Waterfall* 8685 (MO); ELLIS CO.: Wolf Creek, near Shattuck, *Stevens* 2908 (DS, MO, US); TILLMAN CO.: Frederick, *Duncan* s.n. (MO); WOODS CO.: Waynoka dunes, north at Cimarron R. near Highway 281, *Hansen* s.n. (US); WOODWARD CO.: w/o locality, *White* s.n. (MO). **Texas:** ANDREWS CO.: W of Andrews, *Gentry* 1928 (ARIZ); BAILEY CO.: 2 miles S of Muleshoe, *Ferris & Duncan* 3411 (CAS, DS, MO); CHILDRESS CO.: 10½ miles N of Childress, *Cory* 50140 (DS, GH, US); COLLINGSWORTH CO.: 10 miles NE of Wellington, *Cory* 50166 (GH, US); CRANE CO.: near Crane, *Cutak* 6 (MO); CULBERSON CO.: 13 miles E of Van Horn, *Waterfall* 5473 (CAS, GH, MO); DALLAM CO.: Texline, *Howell* 147 (US); ECTOR CO.: Odessa, *Harad* s.n. (US); EL PASO CO.: 25 miles E of El Paso, *Gooding & Hardies* 2860 (ARIZ); GAINES CO.: Seminole, *Tharp* 4558 (TEX, US); GRAYSON CO.: Denison, *Letterman* s.n. (F); HARDEMAN CO.: 7.2 miles N of Quanah on Red River, *Whitehouse* 10751 (UC, US); HARTLEY CO.: 10 miles E of Romero, *Cory* 16468 (GH); HEMPHILL CO.: near Canadian, *Eggert* s.n. (MO); HUDSPETH CO.: 4 miles E of Hueco, *Waterfall* 3865 (ARIZ, GH, MO); LAMB CO.: 16 miles N of Littlefield, *Turner & Melchert* 4829 (TEX); LIPSCOMB CO.: Lipscomb, *Howell* 56 (US); LOVING CO.: 3 miles E of Red Bluff

Lake, *Hinckley & Hinckley* 351 (TEX); LUBBOCK CO.: Lubbock, *Tharp* s.n. (MO, TEX); MITCHELL CO.: 2½ miles N of Colorado City, *Shinners* 8395 (GH, MO); MOTLEY CO.: 5 miles N of Matador, *Cory* 16096 (GH); OLDHAM CO.: 1 mile N of bridge over Canadian R. on Amarillo-Dalhart Rd., *Ferris & Duncan* 3501 (CAS, DS, MO); POTTER CO.: Amarillo, along R. R., *Palmer* 12543 (GH, MO, US); ROBERTS CO.: 28 miles S of Perryton, *Wallis* 7908 (TEX); WARD CO.: 3½ miles NW of Monahans, *Cory* 51973 (US); WILBARGER CO.: *Reverchon* 1230 (F); WINKLER CO.: 9 miles E of Kermit, *Correll* 15190 (US).

MEXICO. **Chihuahua:** 8 miles S of Samalayuca, *Johnston* 3005 (TEX); sand dunes, *Le Sueur* 65 (CAS, F, GH, MO, TEX, US); near Lake Santa Maria, *Nelson* 6404 (GH, US); Colonia Diaz, *Nelson* 6463 (GH, US); sand hills near Paso del Norte, *Pringle* 761 (F, GH, MICH, MO, UC, US); E of Santa Maria, *Schott* s.n. (GH); 36 miles S of Ciudad Juarez, *Shreve* 7921 (ARIZ).

Palafoxia sphacelata is sympatric over part of its range with the eradiate *P. rosea* var. *macrolepis*. In fruiting specimens it is difficult to distinguish between these taxa. However, they are quite distinct, the former possessing dimorphic achenes (the pappus of the ray and disc florets differ) and a chromosome number of $n = 12$; the latter having uniform achenes and a chromosome number of $n = 10$. This, of course, largely precludes serious consideration of Shinners' suggestion (1952) that *P. sphacelata* is "Perhaps better regarded as a third variety of *P. texana*, from which it is very difficult to distinguish after the ray florets have fallen."

Early workers, as indicated by the synonymy above, frequently confused the allopatric *Palafoxia sphacelata* and *P. hookeriana*. Indeed, the species are quite similar and, except for the lower habit and western distribution of the former, are difficult to distinguish. Both species are diploid with $n = 12$, and are probably derived from the same phyletic stock. For additional discussion see *P. hookeriana*.

3. **Palafoxia hookeriana** T. & G. Fl. N. Am. **2**: 368. 1842. TYPE: UNITED STATES. **Texas,** *Drummond* II. 136 (Holotype, K!; Isotypes, GH!, NY!, TEX!).

Polypteris hookeriana (T. & G.) Gray, Proc. Am. Acad. **19**:30. 1883. *Othake hookerianum* (T. & G.) Bush, Trans.

Acad. Sci. St. Louis 14:177. 1904. Hooker (1837) first described and pictured this plant, but erroneously assumed that Drummond's collection was *Palafoxia texana* DC. In his description of the specimen which accompanies the plate, he states: "Flowers large, handsome, distinctly rayed, of which circumstance DeCandolle takes no notice; but in other respects his description is so accurate that I cannot but think the two plants are the same." Gray, in describing the plant as a new species, typified the taxon by reference to Hooker's plate which was made from the Drummond collection cited above.

Polypteris maxima Small, Fl. S.E. U. S. 1288. 1903. TYPE: UNITED STATES. **Texas,** without date or collection number, but collected probably in Austin Co., near Industry, August, 1844, *Lindheimer* (Holotype, NY!; probable isotypes, MO!, NY!). *Othake maximum* (Small) Bush, Trans. Acad. Sci. St. Louis 14:179. 1904.

3a. **Palafoxia hookeriana** T. & G. var. **hookeriana.** Fig. 7.

Plants annual, 25-180 cm tall; stems erect, sparingly branched (except following injury), densely glandular-pubescent (viscid) throughout; midstem leaves narrowly to broadly lanceolate, 4-25 mm wide, 50-100 mm long, with petioles 5-25 mm long, blades gradually tapering into an acute apex, scabrous on both surfaces and usually glandular-pubescent, especially along the margins; inflorescence a few-flowered cyme of 3-8 heads; heads radiate, broadly turbinate, 15-20 mm across (excluding the projecting rays), 15-20 mm high, 30-80 flowered, on densely glandular peduncles 2-10 cm long; principal involucral bracts 10-15, broadly linear to narrowly obovate, 10-15 mm long, 3-5 mm wide, scabrous to densely glandular pubescent, the outer-most rarely becoming somewhat foliaceous; ray florets 8-13, deep pink, 10-20 mm long, the ligule prominently 3-lobed, to 12 mm long and 4 mm wide, the tube narrowly cylindric, 6-9 mm long; disc florets deep pink, 10-12 mm long, tube cylindric ca. 5 mm long, the 5 linear lobes united for ca. 1/3 to 2/5 their length into a funnelform throat;

style branches 3-5 mm long; achenes black, narrowly obpyramidal, 6-8 mm long, sparsely pubescent to nearly glabrous; pappus scales dimorphic, those of the ray obovate, truncate, 0.5-0.7 mm long, those of the disc linear-lanceolate, 5-8 mm long, with pronounced midribs; chromosome number, $n = 12$.

Fig. 7. *Palafoxia hookeriana* var. *hookeriana*. A. Whole plant, ×¼. B. Ray floret, ×2. C. Disc floret, ×3.

Distribution: Relatively light, sandy soils in pine and oak woodlands of southcentral and eastern Texas. Flowering, Aug.-Nov. Fig. 8.

REPRESENTATIVE SPECIMENS. UNITED STATES. **Texas:** AUSTIN CO.: Industry, *Lindheimer* (MO); BASTROP CO.: Bastrop, *Tharp* 44499 (GH, TEX); BURLESON CO.: Lyons, *Martin* 6235 (TEX); CALDWELL CO.: near Luling, *Schulz* s.n. (F); GOLIAD CO.: Goliad, *Williams* 121 (F);

GONZALES CO.: *Whitehouse* s.n. (MO, UC); GRIMES CO.: Navasota, *Fisher* 32153 (ARIZ, CAS, MICH, US); HARRIS CO.: Crosby, *Fisher* 31 (US); HILDALGO CO.: Edinburg, *Shiller* 837 (US); JACKSON CO.: w/o locality, *Drushel* s.n. (TEX); KENEDY CO.: 25 miles S of Sarita, *Webster & Wilbur* 3089 (US); LAVACA CO.: 14 miles SE of Yoakum, *Turner & Tharp* 3273 (TEX); LEE CO.: *Knoblock* s.n. (TEX); LIBERTY CO.: Romayer, *Fisher* 33209 (ARIZ, CAS, F, TEX); NUECES CO.: Flour Bluff, *Parks* s.n. (MO); SAN PATRICIO CO.: 2½ miles NE of Calallen, *Cory* 20678 (GH); STARR CO.: 2.9 miles SW of Santa Elena, *Johnston* 541430 (TEX); VICTORIA CO.: Victoria, *Bindewald* s.n. (TEX); WASHINGTON CO.: 5 miles NE of Brenham, *Turner* 3917 (TEX); WILSON CO.: Cover Ranch, Kicaster, *Parks* 1504 (MO).

This is a handsome species, and while it shows great variation in growth habit, it is nonetheless restricted in its habitat to the forested, deep sandy soils of southcentral and east Texas. It can apparently survive and spread into other areas for, in 1955, the senior author found the species growing as a weed locally in Lucedale, Mississippi, where it was introduced by seed obtained from natural populations in Texas by the local Methodist preacher.

Early workers tended to confuse *Palafoxia hookeriana* with *P. sphacelata*, the latter being a much smaller plant confined to the sandy grasslands of more western regions. Nevertheless, the rayed species, *P. hookeriana* ($n = 12$), *P. sphacelata* ($n = 12$) and *P. reverchonii* ($n = 12$) are clearly related and probably form a monophyletic unit from which the aneuploid derivatives, *P. texana* ($n = 11$), *P. rosea* ($n = 10$), and *P. callosa* ($n = 10$) had their origin, presumably by aneuploid reduction from an ancestral base of $x = 12$.

Palafoxia hookeriana var. *hookeriana* is a relatively rare taxon as is the var. *minor*. We have not seen the two taxa growing together (although Shinners, 1952, indicates they do) and it appears that the latter occurs more often in central Texas while var. *hookeriana* is more widespread, especially to the south.

It is suspected that the rare hybrid between *Palafoxia hookeriana* and *P. reverchonii* must occur since their

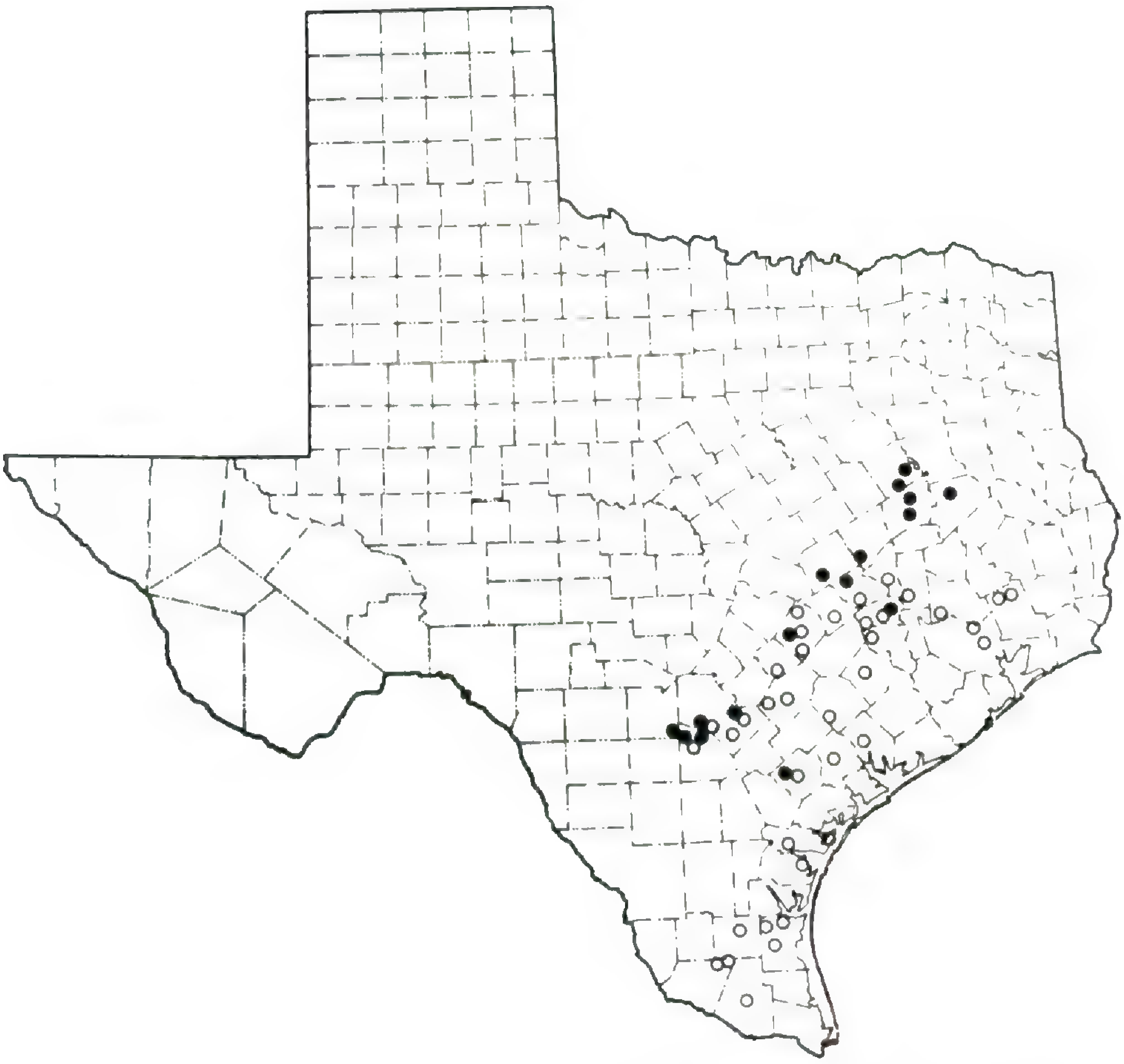

Fig. 8. Distribution of *Palafoxia hookeriana* var. *hookeriana* and *P. hookeriana* var. *minor*.

ranges overlap to the northeast, although we have not found evidence for this in the field. It may be, however, that the less glandular, smaller-headed plants, here recognized as *P. hookeriana* var. *minor*, are from populations which show introgression from *P. reverchonii* into *P. hookeriana*. In the early stages of the present study it was thought possible that the plants called *P. reverchonii* were hybrids between *P. rosea* ($n = 10$) and *P. hookeriana* ($n = 12$), but more recent field work has indicated that these taxa, while often growing near each other, do not hybridize to any detectable extent.

3b. **Palafoxia hookeriana** var. **minor** Shinners, Field & Lab. 20:98. 1952. TYPE: UNITED STATES. **Texas:** HARRIS CO.: Channelview, *Fisher* 50717 (Holotype, SMU!).

Similar to var. *hookeriana* except that the plants are not as robust, possessing smaller heads and less glandular-pubescent stems.

Distribution: Southcentral and eastern Texas on light sandy soils in pine and oak woodland. Flowering, Sept.-Oct. Fig. 8.

REPRESENTATIVE SPECIMENS. UNITED STATES. **Texas:** ATASCOSA CO.: Pleasanton, *Palmer* 10781 (DS, MO, US); 12 miles N of Pleasanton, *Cory* 15564 (GH); Poteet, *Parks* 1270, 1277, 1278, 1416 (MO); BASTROP CO.: W of Cistern, *Tharp & Graham* s.n. (TEX); BEXAR CO.: Applewhite road, 18 miles S of San Antonio, *Clare* 448 (CAS, UC); FREESTONE CO.: 11 miles ESE Fairfield, *Turner* 4443 (TEX); GOLIAD CO.: near Goliad, *Williams* 74 (F, MO); LEON CO.: 5 miles E of Buffalo, *Gould* 7273 (TEX); MEDINA CO.: 3 miles SW of Devine, *Cory* 11756 (GH); MILAM CO.: Milano, *Joor* 54 (MO, UC, US); ROBERTSON CO.: Hearne, *White* s.n. (TEX); WASHINGTON CO.: w/o locality, *Tharp* s.n. (TEX, US); WILSON CO.: Sutherland Springs, *Parks* 15463 (GH).

Shinners (1952), in his key to species, describes the stems of both var. *hookeriana* and var. *minor* as being "glandular-pubescent throughout with widely spreading hairs." Actually the lower half of the main stem of var. *minor* is usually without glandular trichomes and we find this character to be an easy one for distinguishing between the taxa. Also, occasional plants (*Cory* 15563, TEX; *Cory* 15564, GH) may be found without glands on their stems (or involucre!) but these cannot be confused with the more eastern *Palafoxia reverchonii* because they invariably have much broader leaf blades and a coarser, more hispid pubescence. Such plants may represent the occasional hybrid of *P. hookeriana* ($n = 12$) with *P. rosea* ($n = 10$) or *P. texana* ($n = 11$), but we have not observed the former growing together with either of the latter in the field. Baltzer annotated such specimens (e.g., *Palmer* 10781) as *P. sphacelata*, but that is a species of more western distribution.

4. **Palafoxia feayi** Gray, Proc. Am. Acad. 12:59. 1877. *Fig. 9.* TYPE: UNITED STATES. **Florida:** S. Florida, *Feay* s.n. (Holotype, GH!). On the same sheet with collections of the species by Chapman and Curtis.

Spindly shrubs, 1-3 m tall; stems sparingly branched, strigillose to nearly glabrous; leaves simple, opposite or subopposite at first, becoming alternate; mid-stem leaves ovate to narrowly elliptic, 2-6 cm long, 0.5-2.5 cm wide, petioles 2-6 mm long, blades thick, scabrous or roughly hispid on both surfaces, rounded or broadly obtuse at the apex; inflorescence corymbose with 10-50 heads; heads turbinate, 1-2 cm across, 2.0-2.5 cm high (including the exserted florets), 15-25 flowered, on ultimate peduncles 1-4 cm long; principal involucral bracts 9-12, linear to oblong, 5-9 mm long, 1.0-1.5 mm wide, membranous to somewhat thickened, strigillose, usually purplish-tinged; florets regular, white at first, becoming pinkish, corolla about 10 mm long, tube 2 mm long, the throat elongate, cylindric, 4.5-6.0 mm long, the lobes equal, 1.0-1.5 mm

Fig. 9. *Palafoxia feayi.* A. Top of plant, ×¼. B. Head, ×1.

long; style branches 5 mm long, otherwise as described for the genus; achenes obpyramidal, linear, 6-8 mm long, 4-sided, sparingly pubescent with short, spreading hairs; pappus scales 8, 1.5-2.0 mm long, acute to narrowly obtuse at the apex, those on the angles longer; chromosome number, $n = 12$.

Distribution: Sandy soils of pinelands in central and southern Florida usually in open fields with secondary shrubby growth. Flowering, Apr.-Nov., but most commonly in the summer and fall. Fig. 10.

REPRESENTATIVE SPECIMENS. UNITED STATES. **Florida:** BREVARD CO.: Merritts Island, w/o collector, C21264 (US); COLLIER CO.: Marco, *Hitchcock* 159 (F, GH, MO, US); DADE CO.: Arch Creed Prairie, *Small et al.* 6811 (GH, US); DIXIE CO.: Manatee, *Tracy* 6357 (MO, US); HIGHLANDS CO.: Archbold Biological Station, 10 miles S of Lake Placid, *Brass* 15233 (GH, US); HILLSBOROUGH CO.: Riverview, *Blanton* 6718 (DS, F); LAKE CO.: 1 mile E of Lisbon, *Turner* 4663 (TEX); LEE CO.: Fort Myers, *Buswell* 0061 (ARIZ); MANATEE CO.: Palma Sola, *Tracy* 6932 (F, MO, US); ORANGE CO.: Clarcona, *Meislahn* 73a (US); PALM BEACH CO.: w/o locality, *Randolph* 157 (GH); PINELLAS CO.: near St. Petersburg, *Deam* 2814 (MICH); POLK CO.: Winter Haven, *McFarlin* 3325 (MICH); VOLUSIA CO.: near Seville, *Curtis* 6688 (GH, MO, UC, US).

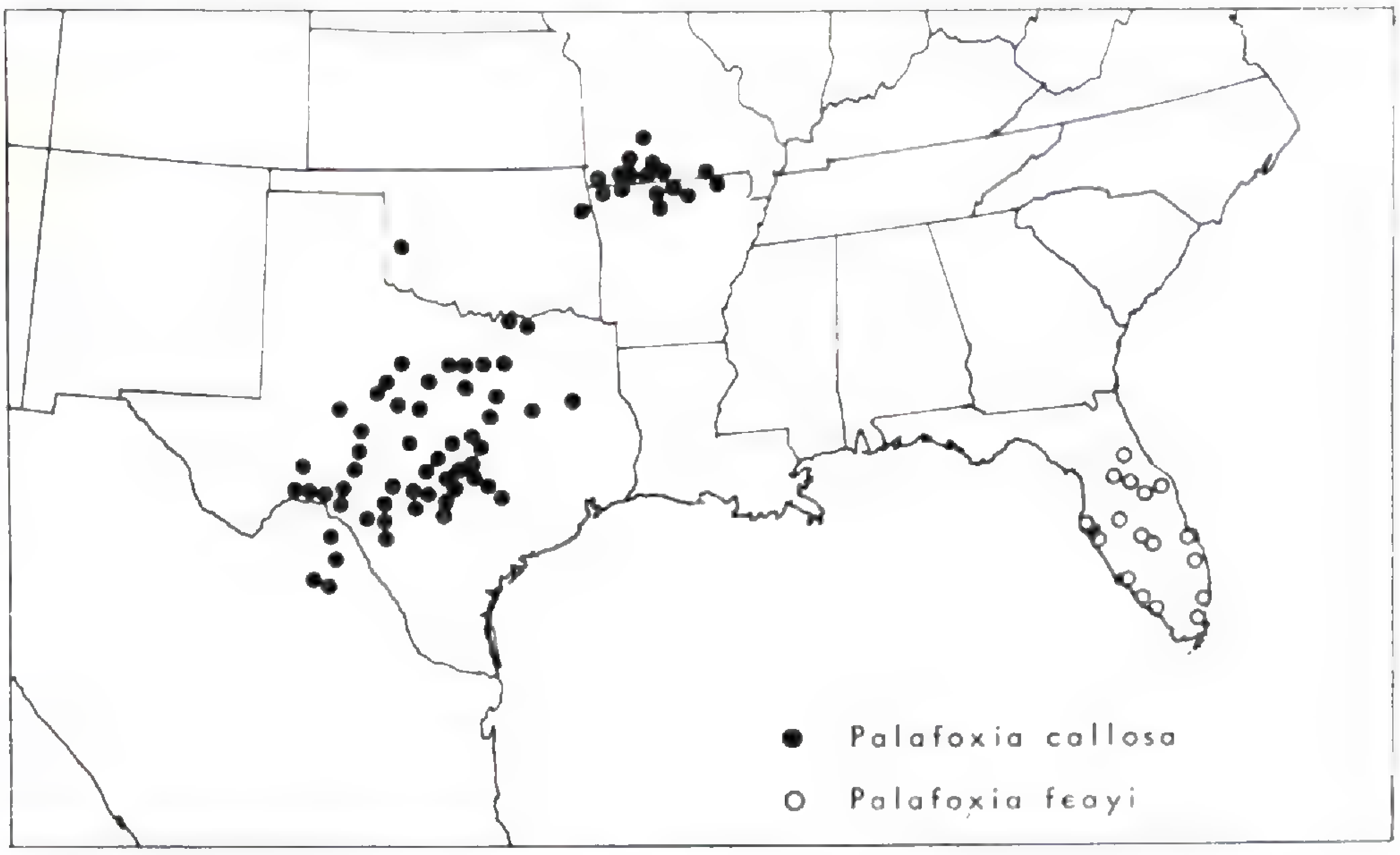

Fig. 10. Distribution of *Palafoxia callosa* and *P. feayi*.

Baltzer (1944) stated that "this species is intermediate between the genera *Polypteris* and *Palafoxia*, but is placed in the latter group because of the floret characters." In our opinion, the species is perhaps as close to *Othake* as it is to *Polypteris* (which includes only *P. integrifolia*).

Palafoxia feayi is a brittle-stemmed shrub up to 3 meters tall. Judging from its restriction to sandy soils on the Florida Peninsula, we believe that its woody nature is secondary, this having developed because of ancestral insular conditions to which it became adapted. Similar robust habits in coastal or active inland dunes have apparently developed independently in *P. texana* var. *robusta* and *P. arida* var. *gigantea*, and it seems almost certain that the robust *P. lindenii* developed from an ancestral stock not too unlike the herbaceous *P. texana*. Nonetheless, *P. feayi* must be older than any of these insular taxa since it has floral features which mark it as quite removed from any of the extant species of *Palafoxia*. In any case it is quite removed geographically from its most closely related taxa, *P. riograndensis* and *P. arida*.

5. **Palafoxia integrifolia** (Nutt.) Torr. & Gray, Fl. N. Am. 2:368. 1842. *Fig. 11.*

Polypteris integrifolia Nutt., Gen. N. Am. Pl. 2:139. 1818. *non* DC., Prodr. 5:659. 1836. TYPE: UNITED STATES. "Georgia" (probably collected in what is now Florida), *Baldwin* s.n. (Holotype, PH!). *Hymenopappus integrifolium* (Nutt.) Spreng., Syst. 3:449. 1826. *Paleolaria fastigiata* Less., Syn. Comp. 156. 1832. *Palafoxia fastigiata* (Less.) DC., Prodr. 5:125. 1836.

Lomaxeta verrucosa Raf., New Fl. Am. 4:72. 1836. *nom illeg.*

Plants perennial, 50-100 cm tall, stems suffruticose, erect to suberect from woody rootstocks or short rhizomes; usually simple below and divaricately branched above; leaves simple, entire, thick, opposite to sub-opposite below, becoming alternate above, scabrous on both surfaces; mid-

stem leaves 3-7(-9) cm long, 0.5-1.0 cm wide, broadly linear to somewhat lanceolate, with petioles 5-10 mm long; inflorescence corymbiform with 10-40 heads; heads broadly turbinate, 10-15 mm high, 7-10 mm across, 10-12 flowered, on ultimate peduncles 2-6 cm long; involucral bracts rounded at the apex, markedly gradate in 2-3 series, membranous, the outer phyllaries short and spreading or somewhat reflexed; florets regular, white to purplish-white; corolla about 12 mm long, deeply 5 lobed, the lobes 4-5 mm long, throat 1.0-1.5 mm long, tube 5-6 mm long; style branches 3.5-5.0 mm long, 4-sided, somewhat tangentially compressed in peripheral florets, minutely pubescent to nearly glabrate; pappus of 10 lanceolate scales, 6-7 mm long, with conspicuous thickened midribs and membranous margins; chromosome number, $n = 12$.

Fig. 11. *Palafoxia integrifolia.* A. Top of plant, ×¼. B. Head, ×1½.

Distribution: Throughout most of Florida, usually in sandy scrubland, or dry pine barrens. Flowering, May-Nov., but most commonly in the late summer and fall. Fig. 5.

REPRESENTATIVE SPECIMENS. UNITED STATES. **Florida:** ALACHUA CO.: Sugarfoot near Gainesville, *Murrill* s.n. (MO); BRADFORD CO.: New River, *Hitchcock* s.n. (F); BREVARD CO.: Indian River region, *Fredholm* 5623 (GH, MO, US); CALHOUN CO.: w/o locality, *Chapman* s.n. (MO); CITRUS CO.: w/o locality, *Hitchcock* s.n. (F); COLUMBIA CO.: Lake City, *Fla. Agric. Col.* 1308 (F); DADE CO.: Miami, *Tracy* 8929 (GH, TEX, US); DUVAL CO.: near Jacksonville, *Curtiss* 1507 (F, GH, MICH, MO, US); GULF CO.: near Apalachicola, 15 Oct. 1890, w/o collector 791a (GH, MO, US); HERNANDO CO.: vicinity of Brooksville, *Jones* 154 (US); HIGHLANDS CO.: Sebring, *Brass* 18146 (GH, US); HILLSBOROUGH CO.: Plant City, *Blanton* 6806 (CAS, TEX); LAKE CO.: vicinity of Eustis, *Nash* 1191 (GH, MICH, MO, UC, US); LEON CO.: 8 miles S of Tallahassee, *Turner* 4657 (TEX); LEE CO.: Fort Myers, *Buswell* 0881 (ARIZ); LIBERTY CO.: between Quincy & Bristol, *Mohr* 1818 (US); MADISON CO.: 9 miles E of Greenville, *Godfrey* 53992 (GH); MANATEE CO.: near Bradenton, *Simpson* 61 (F, MICH, US); MARION CO.: near Ocala, *Palmer* 35186 (GH); ORANGE CO.: S of Orlando, *Bright* 3953 (US); PASCO CO.: New Port Richey, *O'Neill* 1171 (MO); PINELLAS CO.: near St. Petersburg, *Deam* 2826 (MICH, US); POLK CO.: w/o locality, *Ohlinger* 394 (F, MO); PUTNAM CO.: Crescent City, w/o collector (MO); SEMINOLE CO.: Longwood, *Beardslee Jr.* s.n. (UC); VOLUSIA CO.: 2 miles N of Ormond, *Butts* s.n. (GH, UC).

Palafoxia integrifolia was treated as the only species of the genus *Othake* by Baltzer (1944), a treatment also accorded the species by Bush (1904) in his revision of *Othake*. While it is unquestionably the "oddball" of *Palafoxia*, it is, nonetheless, by its floral features and chromosomes, so closely related to *Palafoxia* that little is gained by placing the species in a genus of its own.

6. **Palafoxia linearis** (Cav.) Lag. Elench. Pl. Hort., Matr. 26. 1816. Gen. et Sp. Nov. 26. 1816. TYPE: possible fragments of isotype examined (F). "Ex antiguo herbario generali Herbarium Horti Botanici Matritensis." The plate accompanying the original description matches the material cited (see discussion below).

Fig. 12. *Palafoxia linearis* var. *linearis*. A. Top of plant, ×¼.

6a. **Palafoxia linearis** (Cav.) Lag. var. **linearis.** Fig. 12.

Ageratum lineare Cav., Ic. 3:3. 1794. *Stevia linearis* Cav., Ic. 4:32. *Stevia linearis* (Cav.) Willd., Sp. Pl. 3: 1774. 1804. *Stevia lavandulaefolia* Willd. ex DC., Prodr. 5:125. 1836. As synonym.

Paleolaria carnea Cass., Bull. Soc. Philom. 1818:17. 1818.

Palafoxia leucophylla Gray, Proc. Am. Acad. 8:291. 1870. TYPE: MEXICO. **Baja California:** Carmen Island, *Palmer* 2 (Holotype, GH!; isotypes, NY!, US!). *Palafoxia linearis* var. *leucophylla* (Gray) I. M. Johnston, Proc. Calif. Acad. Sci. 12:1202. 1924.

Palafoxia arenaria Brandg., Proc. Calif. Acad. Sci. 2:178. 1889. TYPE: MEXICO. **Baja California:** Boca de Las Animas, *Brandegee* s.n. (Holotype, UC!; isotypes, GH!, US!).

Plants perennial, 40-80 cm high, up to 150 cm across; stems suffruticose and branched from the base forming conspicuous clumps, rather evenly pubescent with stiff appressed white hairs, glandular, if at all, only in the inflorescence; leaves simple, succulent, alternate; mid-stem leaves lance-linear to nearly obovate, 25-50 mm long, 3-8 mm wide, with petioles 3-8 mm long, blades rather abruptly terminated by an obtuse or rounded apex (very rarely nearly acute), canescent-scabrous on both surfaces; inflorescence a subcorymbose cyme with 3-15(-20) heads; heads subturbinate to nearly cylindric, 5-10 mm across, 20-22 mm high (including the projecting flowers), 10-20 flowered, on ultimate peduncles 1.5-5.0 cm long; principal involucral bracts 8-14, linear, 10-15 mm long, 1-2 mm wide, scabrous-pubescent, especially below (rarely somewhat glandular); florets white with faint tinge of magenta-pink on lobes, regular (outer florets becoming zygomorphic); corolla 7-10 mm long, tube 2-3 mm long, throat cylindric (in outer florets somewhat flaring), 5-7 mm long, the lobes 1-2 mm long; style branches 4-5 mm long, otherwise as described for the genus; achenes 7-11 mm long, linear, 4-sided, densely appressed pubescent; pappus scales 4-8, unequal, with pronounced mid-ribs, the inner florets normally with 4 linear, acute scales, 6-9 mm long on the angles, these alternating with 4 shorter, obtuse or truncate scales of varying lengths (often nearly absent); chromosome number not determined.

Distribution: Dune sand along the eastern sea shore of southern Baja California; also in dunes along the shore of Sonora and Sinaloa. Flowering, Nov.-May, depending on rains. Fig. 13.

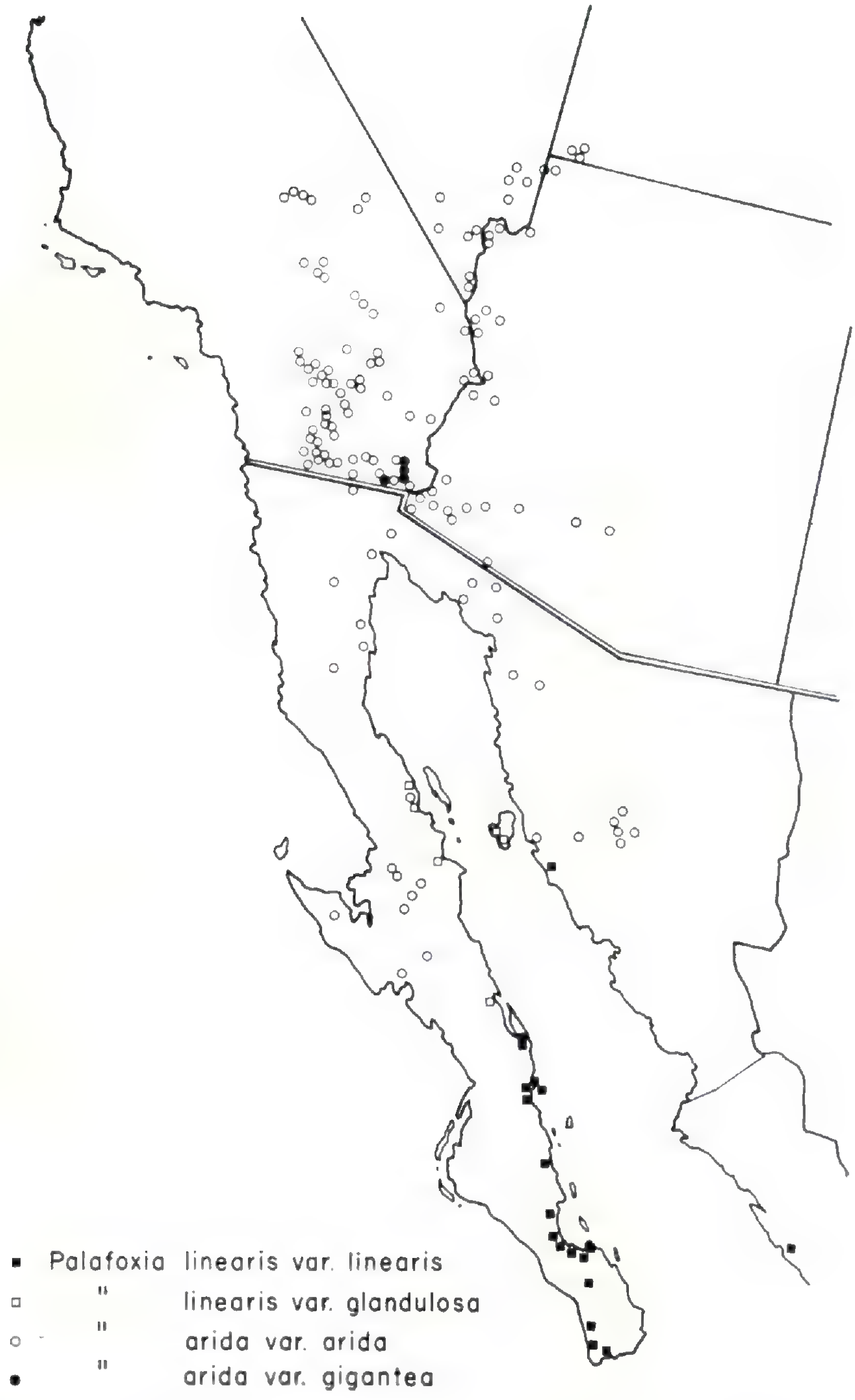

Fig. 13. Distribution of *Palafoxia linearis* var. *linearis*, *P. linearis* var. *glandulosa*, *P. arida* var. *arida*, and *P. arida* var. *gigantea*.

REPRESENTATIVE SPECIMENS. MEXICO. **Baja California:** 18 miles S of Todos Santos, *Carter & Chisaki* 3612 (DS, UC, US); El Mogote, *Carter* 2722 (DS, MO, UC, US); Monserrate Island, *Johnston* 3866 (DS, GH, UC, US); Loreto, *Johnston* 3776 (CAS, GH, MO, UC, US); La Paz, *Jones* 24065 (ARIZ, F, MICH, UC); 17 miles S of Rancho Venancio, *Shreve* 7190 (ARIZ, DS, F, MICH, US); between La Buca and La Ballena, *Wiggins* 5552 (CAS, DS, GH, MICH, UC, US). **Sinaloa:** Altata, *Gentry* 5406 (ARIZ, DS, GH, MICH, MO). SONORA: San Pedro Bay, *Johnston* 4322 (CAS).

Palafoxia linearis has long been used for the more northern, Sonoran desert taxon, *P. arida* (Turner & Morris, 1975).

Wiggins (5552, DS) describes the species as "perennial, leaves very fleshy, corolla white with faint tinge of magenta pink." *Palafoxia linearis* is undoubtedly related to the more widespread *P. arida,* presumably having arisen out of that species in the distant past as a strand-line element.

6b. **Palafoxia linearis** var. **glandulosa** B. L. Turner & M. I. Morris, Madrono 23(2):79-80. 1975.

TYPE: MEXICO. **Baja California:** mouth of arroyo along beach at Barril, 48 miles E of Pozo Aleman, *Wiggins* 7825 (Holotype, DS!; isotypes, F!, GH!, UC!, US!).

Similar to the var. *linearis* except that the stems and leaves are densely covered with a very rough glandular pubescence; in addition the alternating, abortive pappus scales are shorter (like those of *P. arida* var. *arida*).

Distribution: Coastal dune sands of eastern Baja California from latitude 26° 30′ N to 29° 30′ N. Flowering, Dec.-May. Fig. 13.

REPRESENTATIVE SPECIMENS. MEXICO. **Baja California:** Freshwater Bay, Tiburon Island, *Johnston* 3264 (CAS, GH, NY, UC, US, in part); Las Animas Bay, *Johnston* 3514 (CAS, GH, UC, US); San Francisquito Bay, *Johnston* 3588 (CAS, US); San Nicholas Bay, *Johnston* 3716 (MO); Los Angeles Bay, *Palmer* 581 (GH).

Wheeler annotated most of the material cited above as intermediate to *Palafoxia linearis* var. *linearis* and *P. arida* var. *arida* (as treated here). *Palafoxia linearis* var. *glandulosa* is closer in total characters to the former taxon and occupies a similar, but more northern habitat. Johnston apparently found both *P. linearis* var. *linearis* and *P. linearis* var. *glandulosa* growing mixed in two of the localities cited above (*Johnston* 3716; 3264). We could not detect any clear intergradation from specimens collected by Johnston at these localities, although it is suspected that there might be a clinal intergradation from north to south along the shore line.

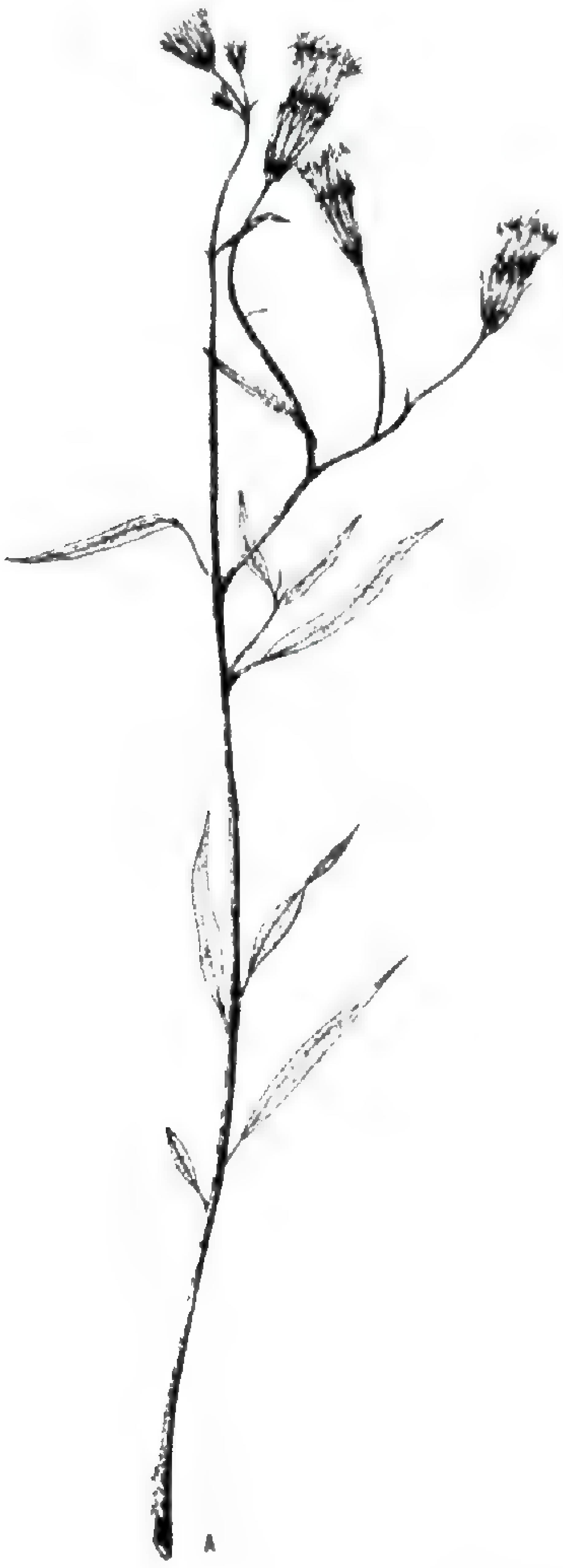

Fig. 14. *Palafoxia arida* var. *arida*. A. Top of plant, ×¼.

7. **Palafoxia arida** B. L. Turner & M. I. Morris, Madrono 23(2):79-80. 1975. TYPE: UNITED STATES. **California:** SAN BERNARDINO CO.: The Needles, *Jones* 3849 (Holotype, US!; isotypes, ARIZ!, CAS!, DS!, F!, NY!, UC!).

7a. **Palafoxia arida** B. L. Turner & M. I. Morris var. **arida.** Fig. 14.

Palafoxia linearis var. *linearis* of authors. *Non Palafoxia linearis* (Cav.) Lag.

Plants annual, 10-70 cm tall; stems erect and usually divaricately branched throughout, scabrous and/or with a rough pubescence (rarely nearly glabrous), the upper portions usually with conspicuous glandular trichomes; mid-stem leaves linear to lance-linear, 2-8 mm wide, 20-100 mm long, with petioles 5-20 mm long, blades gradually tapering into an acute apex, canescent-scabrous on both surfaces; inflorescence a subcorymbose cyme with 5-40 heads; heads subturbinate to nearly cylindric, 5-10 mm across, 20-28 mm high (including the projecting flowers), 9-20 flowered, on ultimate peduncles 1-5(-7) cm long; principal involucral bracts (6-)7-15, linear 10-20 mm long, 1-2 mm wide, scabrous to densely glandular, often somewhat keeled on the back; florets pinkish-white to pink, the inner ones regular, the corolla 9-11 mm long, the tube 2-4 mm long, the throat cylindric 6-8 mm long, the lobes 1-2 mm long; style branches 4-5 mm long; achenes 10-15 mm long, linear, 4-sided, densely to sparsely appressed pubescent; pappus scales 4-8 unequal, with pronounced mid-ribs, the innermost achenes normally with 4 linear, acute scales on the angles, 8-12 mm long, these alternating with 4, much shorter, abortive scales; outermost achenes with 3-8 separate scales of varying lengths (often completely absent); chromosome number, $n = 12$.

Distribution: Mojave, Colorado and Sonoran deserts of the southwestern United States and Mexico, usually in sandy soils at low elevations. Flowering, Feb.-May (rarely later with rains). Fig. 13.

REPRESENTATIVE SPECIMENS. UNITED STATES. **Arizona:** MARICOPA CO.: Sentinel, *Harrison & Belden* 3556 (ARIZ); MOHAVE CO.: Willow Beach, *Clokey* 5957 (DS, MO, TEX, UC); PINAL CO.: 10 miles W of Casa Grande, *Parker* 8259 (ARIZ); YUMA CO.: 14 miles E of Yuma, *Wolf* 2286 (CAS, DS, GH). **California:** IMPERIAL CO.: near Fish Springs, *Nelson & Nelson* 3293 (DS, GH, MO, UC, US); RIVERSIDE CO.: ca. 12 miles E of Indio, *Hitchcock* 5848 (DS, GH, MO, UC); SAN BERNARDINO CO.: Slate Mountains, *Epling, Ellison & Anderson* s.n. (MICH, MO, US); 5 miles SW of Trona, *Gould* 986 (ARIZ, GH, MO); SAN DIEGO CO.: Coyote Canyon, *Hall* 2768 (DS, MO, UC, US). **Nevada:** CLARK CO.: Logan, *Kennedy* s.n. (CAS, DS, GH, UC, US). **Utah:** WASHINGTON CO.: Red Hill N of St. George, *Hall* 514 (US); Leeds, *Cottam* 5389 (TEX).

MEXICO. **Baja California:** Calamilli, *Brandegee* s.n. (UC); 15.5 km NW of El Arco, *Carter et al.* 1907 (DS, UC, US); 59 km SW of San Ignacio, *Carter et al.* 2514 (DS, MO, UC, US); sand hills of the Viscaino Depression, south and west of Scammon's Lagoon, *Gentry* 7524 (ARIZ, DS, UC); 32 miles S of Pozo Aleman, *Shreve* 7008 (ARIZ, F, GH, MICH, MO); southern part of the Sierra San Pedro Martir, *Wiggins* 9915 (DS, US); 27.4 miles S of Pozo Aleman, *Wiggins* 7863 (DS, F, GH, MICH, UC, US). **Sonora:** Rocky Point, *Clark* 11213 (GH); along Rio de Sonora, Hermosillo, *Drouet & Richards* 3480 (F); 6 km N of Hermosillo, *Drouet & Richards* 3758 (F); E of Villa de Seris along Rio de Sonora, *Drouet, Richards & Alvarado* 3395 (F); Hermosillo, *Eisen* s.n. (US); 173 miles S of Nogales, *Frye & Frye* 2288 (ARIZ, DS, GH, UC); S side of Punta Penasco, *Hammerly* 16 (DS, TEX, UC); 2 miles W of Cabarco, *Keck* 4021 (CAS); 22 miles S of Sonoyta, *Keck* 4161 (DS, US); Cabarco, *Long* 74 (US); Papago Tanks, *MacDougal* 35 (US); Hermosillo, *Maltby* 208 (US); Colorado River at Colonia Diaz, *Mearns* 2831 (DS, US); Lerdo, *Palmer* 940 (GH, UC); 20 miles N of Hermosillo *Parker* 8224 (ARIZ, UC); 4 miles NW of Caborca, *Wiggins* 8231 (DS, GH, MICH, UC, US); 2 miles N of the fishing village on Kino Bay, *Wiggins & Rollins* 167 (ARIZ, DS, GH, MICH, MO).

This relatively common, widespread species has heretofore been called *Palafoxia linearis* by nearly all recent taxonomists working in the desert Southwest. This name, however, applies to a well-marked, related taxon which occurs in southern Baja California, the type apparently having been collected near La Paz. Wheeler, by annotation only, also recognized the two taxa as specifically distinct, correctly restricting the name, *P. linearis*, to the populations from southern-most Baja California. Gray also recog-

nized the taxa as specifically distinct, but contrary to the present Code, proposed the name *P. leucophylla* for the more southern element. Johnston, apparently accepting Gray's nomenclature but not his hierarchial ranking, reduced Gray's synonym to varietal status.

In our opinion, *Palafoxia arida* and *P. linearis* are relatively "clean" species in that they are readily distinguished morphologically, have different, essentially allopatric distributions, and grow under different climatic regimes. At least the two taxa are more distantly related than are certain other allopatric taxa regarded as species by previous workers, as well as by us (e.g., the three closely related species, *P. hookeriana*, *P. sphacelata* and *P. reverchonii*).

7b. **Palafoxia arida** var. **gigantea** (M. E. Jones) B. L. Turner & M. I. Morris, Madrono 23(2):79-80. 1975.

Palafoxia linearis var. *gigantea* M. E. Jones, Contrib. West. Bot. 18:79. 1933. TYPE: UNITED STATES. **California:** W of Yuma, sand dunes, *Jones* 28599 (Holotype, POM!; isotypes, MO!, UC!).

Palafoxia linearis var. *arenicola* Nels., Am. Jour. Bot. 23:265-66. 1936. TYPE: UNITED STATES. **California:** in the sand dunes, Calif., W of Yuma, Arizona, *Nelson* 11161 (Holotype, RM!; isotypes, DS!, MO!).

Plants apparently annual or short lived perennials (described by some collectors as a succulent perennial), 80-200 cm tall; stems erect, branched from the base, the larger branches 0.5-1.0 cm in diameter, glabrous or nearly so; leaves simple, alternate, mid-stem ones lance-linear, 6-12 cm long, 0.7-1.5 cm wide, with petioles 1.0-1.5 cm long, the blades tapering into an acute apex, scabrous on both surfaces; inflorescence a subcorymbose cyme with 10-20 heads; heads subturbinate, 10-20 mm across, 28-35 mm high (including the projecting flowers), 18-40 flowered, on ultimate peduncles 2-7 cm long; principal involucral bracts 10-16, linear, 16-25 mm long, 1.0-2.5 mm wide, scabrous, often somewhat keeled on the back; florets "lavender-white," regular, the corolla 10-13 mm long, the tube 3.0-4.5 mm

long, the throat cylindric, 7-9 mm long, the lobes 1-2 mm long; style branches 4-6 mm long, otherwise as described for the genus; achenes 12-16 mm long, linear, somewhat 4-sided to nearly cylindric, densely short pubescent with closely ascending hairs; pappus scales 4-8, unequal, with pronounced midribs, the innermost achenes normally with 4 linear, acute scales 9-12 mm long, these alternating with 4 much shorter scales, 2-5 mm long; outermost achenes with 3-8 scales of varying lengths; chromosome number, $n = 12$.

Distribution: Restricted to the actively blowing sand hills just west of Yuma, Arizona. Flowering, Feb.-May (often later with rains). Fig. 13.

REPRESENTATIVE SPECIMENS. UNITED STATES. **California:** IMPERIAL CO.: 6 miles W of Winterhaven, *Alexander & Kellogg* 1889 (DS, GH, TEX, UC); sand dunes W of Yuma, *Alexander & Kellogg* 1936 (ARIZ, CAS, DS, GH, MO, TEX, UC); 25 miles W of Yuma, *Munz* 11968 (UC); Holtville, *Munz & Hitchcock* 12131 (DS, F, MO, UC); 16 miles E of Brawly, *Turner* 4759 (TEX); 22 miles W of Yuma, *Wiggins* 8920 (CAS, DS); 2 miles E of Gray's Well on road from Yuma to Holtville, *Wolf* 1888 (DS).

The variety *gigantea* is undoubtedly closely related to *Palafoxia arida* var. *arida* presumably having arisen relatively recently from that taxon (within the time of the formation of the large northwest-southeast trending dune sands in the southern portion of the Coachella Valley, probably about 5000 years ago or less). It is distinguished almost solely by its more robust habit and larger heads. After a visit by the senior author to the type locality, he was reasonably convinced that the variety was a good taxon, primarily because the smaller-headed var. *arida* grows adjacent to, and often upon, some of the lesser dunes in the area, while the larger-headed forms were restricted almost entirely to the dune sands. This is true even in depauperate (less than 0.9 m tall) forms of var. *gigantea*. Blake (1945) also recognized the variety as did Nelson (1936), who presumably was unaware of Jones' (1933) earlier varietal epithet.

Fig. 15. *Palafoxia riograndensis*. A. Whole plant, ×⅓. B. Head. ×2.

8. **Palafoxia riograndensis** Cory, Rhodora 48:84. 1946. Fig. 15. TYPE: UNITED STATES. **Texas:** PRESIDIO CO.: 3½ miles SE of Presidio, *Cory* 31195 (Holotype, GH!; isotype, US!).

Palafoxia cyanophylla Shinners, Field & Lab. 17:23-30. 1949. TYPE: UNITED STATES. **Texas:** BREWSTER CO.: in bare sand, mouth of Santa Elena Canyon, Big Bend National Park, *Shinners* 8792 (Holotype, SMU!).

Plants annual, 30-60 cm tall; stems erect, usually branched from the base, pubescent with stiff white hairs and generally scabrous; leaves simple, alternate, the mid-stem ones linear-lanceolate, 3-7 cm long, 2-8 mm wide, with petioles 5-15 mm long, the blades gradually tapering into an acute apex, white scabrous pubescent on both surfaces; inflorescence a subcorymbose cyme with 5-numerous heads; heads cylindrical-turbinate, 15-25 mm high (including the exserted florets), 4-10 mm wide, 8-25 flowered, on ultimate glandular-pubescent (viscous) peduncles 1.5-6.0 cm long; principal involucral bracts 7-10, narrowly lance-oblong, 10-15 mm long, 1.2-2.0 mm wide, scabrous or hispid on the back; florets "pale pinkish purple" to "purple," outer florets distinctly zygomorphic (but not ligulate), the inner florets nearly regular; corolla 6-9 mm long, tube cylindric, 2.3-4.0 mm long, throat conspicuously pubescent, narrowly funnel-form, 1.5-3.0 mm long, the lobes lanceolate-oblong, 1.8-3.0 mm long; style branches 3-4 mm long, otherwise as described for the genus; achenes linear, 4-sided, obpyramidal, 7-12 mm long, variously hispid, but especially so on the angles; pappus of inner florets composed of 4 lanceolate scales, 5-8 mm long (these often alternating with much smaller, obtuse scales), outer-most florets with abortive pappus scales, these usually fused into an irregular crown; chromosome number, $n = 12$.

Distribution: Dune sand and silty-sandy soils along stream beds of the Chihuahuan desert in north-central Mexico, entering the United States only along the Rio Grande River in Texas. Flowering, Apr.-Nov., depending on rains, but usually in the late summer and fall. Fig. 16.

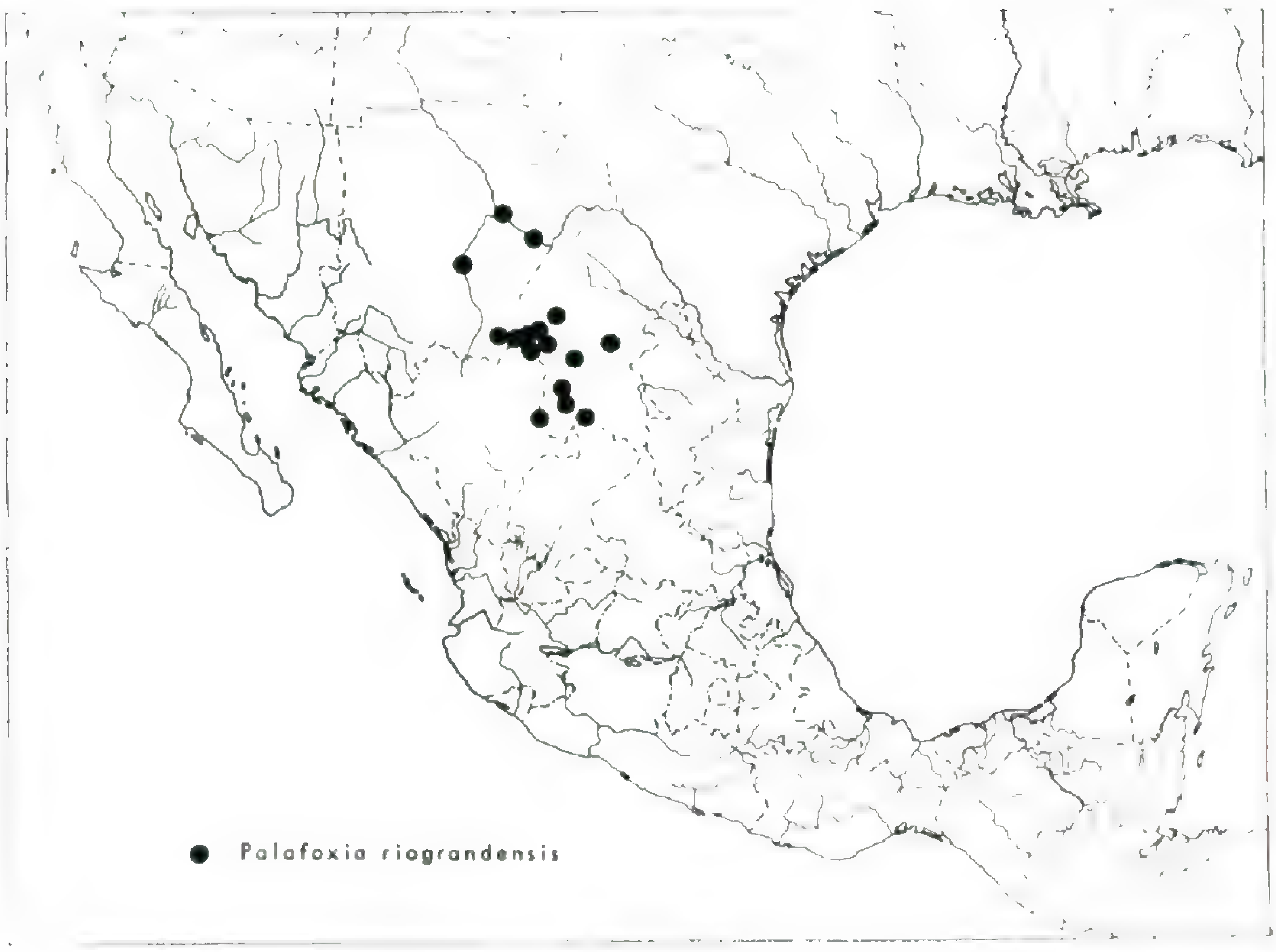

Fig. 16. Distribution of *Palafoxia riograndensis.*

REPRESENTATIVE SPECIMENS. UNITED STATES. **Texas:** BREWSTER CO.: entrance to Santa Elena Canyon, *Warnock* 1160 (GH); near entrance to Santa Elena Canyon, *Sperry* 1160 (US); mouth of Santa Elena Canyon, *McVaugh* 12708 (MICH); PRESIDIO CO.: 2-3 miles E of Presidio, *Hinckley* 3235 (GH, US); 3½ miles SE of Presidio, *Cory* 31195 (US).

MEXICO. **Chihuahua:** 5 miles NE of Laguna Palomas, *Johnston* 7826 (GH); 6 miles NE of Carillo, *Shreve* 8848 (ARIZ, MICH, US). **Coahuila:** 3 miles SW of Torreon on Nazas River, *Fisher* 44125 (GH, MO, NY); Tanque Colorado, road from Zacatosa, SE to Puerto Colorado, *Johnston* 8666 (GH, TEX); Torreon and vicinity, *Palmer* 486 (F, GH, MO, UC, US); Monclova, *Palmer* 643 (F, GH, NY, US); Movano, *Purpus* 4473 (UC); SW end of Laguna del Rey, *Stewart* 3022 (GH); 5 km NE of Las Delicias, *Stewart* 2840 (GH); 1 km SE Las Margaritas, *Stewart* 2946 (GH); 21 miles W of El Oro, *White* 2011 (MICH).

As indicated by Shinners (1952), *Palafoxia cyanophylla* is clearly synonymous with the earlier *P. riograndensis,* although he failed to find that Baltzer (1944) cited a specimen of this taxon (*Palmer* 486, MO) as belonging to *P. linearis* var. *leucophylla.* While *P. riograndensis* is super-

ficially similar to *P. linearis* (as indicated by Shinners), it is clearly distinct. It has the habit of *P. arida*, but possesses quite different floral features (corolla lobes longer than the throat and irregular florets along the periphery of the head).

Palafoxia riograndensis is apparently introduced periodically into Texas along the Rio Grande where it occurs in small populations on sand banks along the river. It presumably washes into the Rio Grande from streams feeding from the more southern sandy areas of the Chihuahuan desert.

9. **Palafoxia lindenii** Gray, Pl. Wright. **1**:120. 1850. Fig. 17. TYPE: MEXICO. **Veracruz:** on sandhills near the sea, *Galeotti* 2627 (Holotype, K!; fragment of holotype, GH!).

Polypteris lindenii (Gray) Gray, Proc. Am. Acad. **19**:30. 1883. *Othake lindenii* (Gray) Bush, Trans. Acad. Sci. St. Louis **14**:173. 1904.

Plants annual, 50-100 cm tall or sometimes appearing perennial and rhizomatous when rooting at the nodes in blown dune sand; stems suffruticose, sparsely branched, suberect to erect, strigillose throughout; leaves entire, simple and opposite at first, becoming alternate above, the mid-stem ones oblong-lanceolate to narrowly elliptic, 4-6 cm long, 5-8 mm wide, thick, puberulent on both surfaces, acute to rounded at the apex, petioles 7-10 mm long; inflorescence corymbose with 3-10 heads; heads turbinate, 1-1.5 cm wide, 1.5-2 cm high (including the extended florets), 18-30 flowered, on ultimate thickened, densely glandular-pubescent peduncles 1.5-6 cm long; involucral bracts 10-15, linear, 8-10 mm long, 1.0-2.5 mm wide, thickened on the back, somewhat scarious along the margins; florets apparently whitish, regular; corolla about 10 mm long, tube glandular-pubescent almost 3 mm long, throat cylindric, 1.5-2.0 mm long, lobes linear, 4-5 mm long; anthers 4 mm long; style branches 3-4 mm long, otherwise as described for the genus; achenes obpyramidal, 5-6(-7)

Fig. 17. *Palafoxia lindenii.* A. Top of plant, ×¼. B. Floret, ×3.

mm long, glabrous or nearly so; pappus of 12 lanceolate scales, 4-5 mm long, acute at the apex, without an extended awn or mucro; chromosome number, $n = 11$.

Distribution: Known from only a few collections about Veracruz, Mexico, where it is apparently confined to dune sands. Flowering, Aug.-Jan., and probably later. Fig. 18.

REPRESENTATIVE SPECIMENS. MEXICO. **Veracruz:** at Veracruz, *Fisher* 122 (CAS, DS, MICH, TEX); Nautla, "vegetacion litoral," *Gold* 121 (NY); near shore, N of Veracruz, *Greenman* 95 (F, GH, NY); Veracruz, Medanos de Perro, *Juzepezuk* 1147 (US); Gulf Coast, *Purpus* 6025 (F, GH, MO, NY, UC, US); shore of Gulf of Mexico near San Carlos, *Purpus* 14168 (F, GH, UC).

The species is undoubtedly related to *Palafoxia texana,* presumably derived out of that species relatively recently through an insular-type adaptation to the dune sands in and about Veracruz, Mexico. Both species are diploid with $n = 11$ and both possess similar head and floral features.

10. **Palafoxia callosa** (Nutt.) T. & G., Fl. N. Am. 2:369. 1842. Fig. 19.

Stevia callosa Nutt., Jour. Acad. Phila. 2:121. 1821. TYPE: UNITED STATES: on the gravelly banks of the Arkansas, rare, *Nuttall* s.n., (Probable holotype, PH!). *Florestina callosa* (Nutt.) DC., Prodr. 5:655. 1836. *Othake tenuifolium* Raf., New Fl. 4:74. 1838. *Polypteris callosa* (Nutt.) Gray, Proc. Am. Acad. 19:30. 1883. *Othake callosum* (Nutt.) Bush, Trans. Acad. Sci. St. Louis 14:174. 1904.

Palafoxia bella Cory, Field & Lab. **16**:62. 1948. TYPE: UNITED STATES. **Texas:** TOM GREEN CO.: 3 miles S of Christoval, *Cory* 50467. (Holotype, SMU!). *Palafoxia callosa* var. *bella* (Cory) Shinners, Field & Lab. **20**:94. 1952.

Plants annual, 20-60 cm tall; stems brittle, slender, or less often, stout and diffusely branched; leaves sessile or shortly petioled, linear, 1-4 mm wide, 20-70 mm long, 1-nerved, strigose-hispidulous on both surfaces; inflorescence corymbose with several to numerous heads, the branches

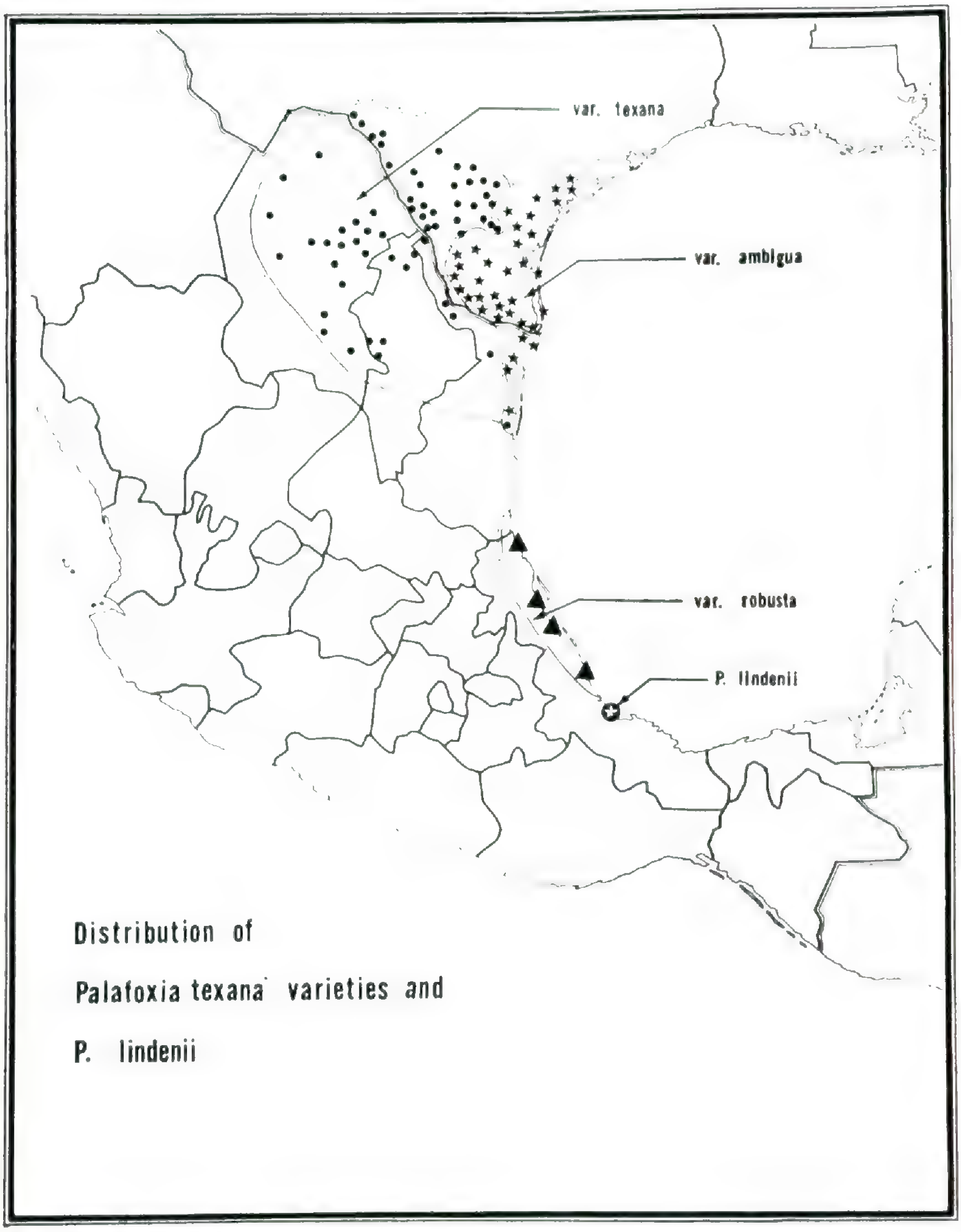

Fig. 18. Distribution of *Palafoxia lindenii*, *P. texana* var. *texana*, *P. texana* var. *ambigua*, and *P. texana* var. *robusta*.

densely black-granular; heads turbinate, 3-6 mm high, 3-5 mm broad, 5-30 flowered, on ultimate peduncles 1-4 cm long; involucral bracts 10-12, linear-oblanceolate, strigose, 3-5 mm long, ca. 1 mm wide; florets lavender, pale-violet (pink) to white, regular, 5-6 mm long, tube 1-2 mm long, the lobes linear, 4-5 mm long; achenes mostly 3-5 mm long, obpyramidal, hirsutulous; pappus scales 8, obovate, 0.3-1.0 mm long; chromosome number, $n = 10$.

Distribution: Calcareous, usually rocky limestone soils from southern Missouri to northeastern Mexico, mostly in juniper glades or in disturbed grasslands. Flowering, Jun.-Nov. Fig. 10.

REPRESENTATIVE SPECIMENS. UNITED STATES. **Arkansas:** BAXTER CO.: Henderson, *Demaree* 28526 (TEX); BENTON CO.: w/o locality, *Bush* 15752 (MO); CARROLL CO.: Beaver, *Palmer* 4492 (MO, US); IZARD CO.: Guion, *Demaree* 23758 (MO, UC); MARION CO.: Bull Shoals Dam Reservoir, *Demaree* 29971 (TEX); RANDOLPH CO.: Noland, *Demaree* 53-790 (TEX); SEARCY CO.: Gilbert, *Emig* 43 (MO). **Missouri:** BARRY CO.: Eagle Rock, *Mackenzie* s.n. (MICH, MO); DOUGLAS CO.: Richville, *Steyermark* 14657 (MO); GREENE CO.: w/o locality, *Bush* 203 (F, GH, MO, UC, US); MC DONALD CO.: Butler Creek, Noel, *Palmer* 4078 (MO, US); OZARK CO.: Tecumseh, *Palmer* 33012 (MO); STONE CO.: Gelena, *Palmer* 4633 (MO, US); TANEY CO.: Swan, *Bush* 476 (GH, MO, UC, US). **Oklahoma:** ADAIR CO.: Westville, *Moore* s.n. (TEX); BECKHAM CO.: 6 miles S of Elk City, *Eskew* 1502 (GH, MO). **Texas:** BANDERA CO.: 4 miles S Pipecreek, *Turner* 3840 (TEX); BASTROP CO.: w/o locality, *Duval* s.n. (TEX); BLANCO CO.: gravel bars of river, *Palmer* 12856 (GH, MO, UC, US); BRAZOS CO.: w/o locality, *Palmer* 10732 (DS); BROWN CO.: near Brownwood, *Palmer* 26816 (GH); BURNET CO.: near Buchanan Dam, *Gentry* 15 (TEX); CHEROKEE CO.: dry hills N of Jacksonville, *Eggert* s.n. (MO); COLEMAN CO.: 1 mile SE of Goldsboro, *Turner* 4860 (TEX); COMAL CO.: New Braunfels, *Lindheimer* 956 (ARIZ, F, GH, MO, TEX, UC, US); CORYELL CO.: near highway along Camp Hood, *Gould* 5371 (TEX); DALLAS CO.: limestone prairies, *Reverchon* 3288 (GH, MO, US); EASTLAND CO.: Ranger, *Robinson* s.n. (TEX); FANNIN CO.: 2 miles SE of Whitewright, *Turner & Tharp* 3131 (TEX); FAYETTE CO.: 4 miles E of La Grange, *Turner* 4452 (TEX); FREESTONE CO.: 12.5 miles ESE of Fairfield, *Shinners* 9633 (TEX); GILLESPIE CO.: Willow Cr., *Jermy* 804 (MO, US); GRAYSON CO.: Denison, *Letterman* s.n. (MO, US); HAYS CO.: near Wimberley, *Warnock* W900 (GH, TEX); HOOD CO.: Comanche Peak near Grabury, *Palmer* 6443 (MO, US); KENDALL CO.:

Fig. 19. *Palafoxia callosa*. A. Whole plant, ×¼. B. Head, ×3.

Spanish Pass, *Clemens & Clemens* 1029 (DS, MO); KERR CO.: Turtle Creek, 13.75 miles W of Kerrville, *Cory* 52417 (DS, UC, US); LAMPASAS CO.: 2 miles S of Lampasas, *Turner* 4587 (TEX); LLANO CO.: 17.6 miles E of Llano, *Turner & Johnston* 2484 (TEX); MC LENNAN CO.: Waco, *Bodin* s.n. (F, UC); PALO PINTO CO.: 9 miles W of Mineral Wells, *Whitehouse* 19242 (MICH, UC, US); PARKER CO.: Weatherford, *Tracy* 8142 (F, GH, MO, TEX, US). PECOS CO.: between Sheffield & Pecos River, *Ferris & Duncan* 2915 (CAS, DS, MO); REAL CO.: along Pulliam Creek near Camp Wood, *Correll* 15203 (US); SCHLEICHER CO.: 9.5 miles N of Eldorado, *Cory* 52513 (DS, UC, US); SOMERVELL CO.: Paluxy Creek, 2 miles above Glen Rose, *Ward* s.n. (US); STERLING CO.: 11 miles NW of Sterling City, *Cory* 50465 (DS, GH, TEX, UC, US); SUTTON CO.: Schoolhouse Hill, Sonora, *Cory* 40835 (TEX); TARRANT CO.: w/o locality, *Ruth* 738 (DS, US); TAYLOR CO.: Abilene State Park, *Tolstead* 7610 (MICH, MO, UC); TOM GREENE CO.: South Concho River, 1.5 miles N of Christoval, *Cory* 52517 (DS, US); TRAVIS CO.: 3 miles NW of Austin, *Warnock* 45-67 (DS, MO, TEX, UC); UVALDE CO.: 2 miles S of Blewett, *Turner* 3866 (TEX); VAL VERDE CO.: 9¼ miles N of Del Rio, *Cory* 20867 (GH); WILLIAMSON CO.: 7 miles W of Round Rock, *York* 46314 (F, MO, TEX, UC).

MEXICO. **Coahuila:** Muzquiz, Santa Anna Canyon, *Marsh* 540 (TEX); 65 miles NW Sabinas, *Gould* 10676 (TEX); 17 miles W of Ciudad Acuna, *Powell et al.* 1411 (TEX); 43 miles NW of Muzquiz, *Powell et al.* 1587 (TEX).

Palafoxia callosa is easily recognized by its linear leaves and narrow turbinate involucre. Some of the larger-headed (i.e., with more numerous florets), paler-flowered, more western populations were recognized as a species, *P. bella*, by Cory but these seem hardly worthy of the varietal recognition accorded the populations by Shinners.

Palafoxia callosa seems closest to *P. rosea*. Both species are diploid with $n = 10$ and while they are partially sympatric in a geographic sense, the former occurs predominantly, or only, on calcareous soils, the latter on siliceous, sandy soils. Synthetic hybrids between the species are easily made, but hybrids or their derivatives have not been observed in the field.

11. **Palafoxia rosea** (Bush) Cory, Rhodora 48:86. 1946. TYPE: UNITED STATES. **Texas:** HARRIS CO.: Sheldon, 18 miles E of Houston, *Reverchon* 3656 (Holotype, MO!; isotypes, GH!, NY!).

11a. **Palafoxia rosea** (Bush) Cory var. **rosea.** Fig. 20.

Othake roseum Bush, Trans. Acad. Sci. St. Louis 14:175. 1904. *Polypteris rosea* (Bush) Small, Fl. S. E. U. S., ed. 2, 1372. 1913.

Annual herbs, 10-50 cm tall; stems brittle, scabrous; leaves simple, opposite at first but soon becoming alternate, the mid-stem ones linear-lanceolate, 2-10 mm wide, 3-6 cm long, petioles 3-15 mm long, blades inconspicuously 3-nerved, scabrous on both surfaces; inflorescence corymbose with mostly 3-10 heads; heads narrowly to broadly turbinate, 6-12 mm across, 10-16 mm high (including disc florets), 10-30 flowered, on ultimate peduncles 1-5 cm long; principal involucral bracts 8-12, oblanceolate, 5-7 mm long, 1.2-3.0 mm wide, often purplish tinged, pubescent with short rough hairs interspersed with glandular capitate trichomes (the latter sometimes absent or nearly so); florets pale-violet, regular 7-10 mm long, the throat 4-5 mm long slit to the base or nearly so, the lobes linear, 4-5 mm long; achenes mostly 5-8 mm long, densely short, appressed pubescent; pappus scales usually 8, 1-3 mm long, scarious except for the prominent midrib, obtuse to acute at the apex; chromosome number, $n = 10$.

Distribution: Sandy soils in eastern Texas. Flowering, May-Nov. Fig. 21.

REPRESENTATIVE SPECIMENS. UNITED STATES. **Oklahoma:** CADDO CO.: 4 miles W of Anadarko, *Hopkins & Nelson* 881 (DS, TEX, UC); COMANCHE CO.: State Fish Hatchery, *Robertson* 106 (TEX); SWANSON CO.: near Mountain Park, *Stevens* 1278 (DS, US). **Texas:** AUSTIN CO.: Industry, *Wurzlow* 35 (US); BRAZORIA CO.: Substation no. 3, Angleton, *Cory* 51081 (DS, GH, UC, US); BRAZOS CO.: 2 miles S of College Station, *Ammerman* 7 (MO, UC); BURLESON CO.: Lyons, *Maite* 6536 (TEX); COLORADO CO.: Eagle Lake, *Biology Class* 41 (TEX); DALLAS CO.: N of Dallas, *Eggert* s.n. (MO); FAYETTE CO.: Muldoon, *Ripple* 51-743 (TEX); FREESTONE CO.: 11.5 miles ESE Fairfield, *Turner* 4447 (TEX); GALVESTON CO.: Moses Lake, 3 miles NW of Texas City, *Turner* 3070 (TEX); HARRIS CO.: 5 miles SE of Genoa, *Cory* 50695 (DS, GH, UC, US); LEE CO.: 1½ miles SW of Giddings, *Cory* 55758 (US); MONTGOMERY CO.: pine woods, *Dixon* 478 (F); SAN JACINTO CO.: Evergreen, *Joor* s.n. (MO); SAN JACINTO CO.: S of Mathis, *Rose*

Fig. 20. *Palafoxia rosea* var. *rosea*, A & B. *P. rosea* var. *macrolepis*, C. A. Top of plant, ×¼. B. Achene and pappus, ×3. C. Achene and pappus, ×3.

& *Russell* 24159 (GH); SAN SABA CO.: Cherokee, *Joor* s.n. (MO); TRAVIS CO.: Austin, *Tharp* 189 (GH, TEX); VICTORIA CO.: 10 miles SW of Victoria, *McVaugh* 12412 (MICH, US); WALKER CO.: SW of Huntsville, *Cory* 50669 (GH); WILBARGER CO.: *Ball* 1230 (F).

This variety is mostly confined to forest areas of eastern Texas and is best distinguished by its smaller heads, with smaller florets and pappus. In central Texas it appears to intergrade with the western populations, which are designated below as var. *macrolepis*. In Llano Co., for example, short and long pappus forms are found in the same population (*Turner & Johnston* 2512, TEX) although the plants possess the larger heads of var. *macrolepis*.

11b. **Palafoxia rosea** var. **macrolepis** (Rydb.) B. L. Turner & M. I. Morris, comb. nov. Fig. 20.

Othake macrolepis Rydb., Bull. Torr. Bot. Club **37**:332. 1910. TYPE: UNITED STATES. **Colorado:** BENT CO.: Rule Creek, *Osterhout* 4097 (Holotype, NY!). *Polypteris macrolepis* (Rydb.) Cory, Rhodora 38:408. 1936. *Othake texanum* var. *macrolepis* (Rydb.) Baltzer. Ann. Mo. Bot. Gard. 31:258. 1944. *Palafoxia texana* var. *macrolepis* (Rydb.) Shinners, Field & Lab. **20**:97. 1952.

Palafoxia rosea var. *papposa* Shinners, Field & Lab. **20**: 95. 1952. TYPE: UNITED STATES. **Texas:** BEXAR CO.: San Antonio, Apicultural Laboratory, *Parks* s.n. (Holotype, TAM!; isotypes, SMU!).

Similar to var. *rosea*, but possessing larger heads and longer pappus.

Distribution: Sandy soils in plains country of south Texas NW to Wyoming. Flowering, May-Sept. Fig. 21.

REPRESENTATIVE SPECIMENS. UNITED STATES: **Colorado:** LAS ANIMAS CO.: 3 miles SW of Tobe, *Rogers* 6128 (TEX). **Kansas:** SUMNER CO.: Caldwell, *Carleton* 340 (US). **New Mexico:** LEA CO.: 21 miles W of Hobbs, *Waterfall* 7837 (GH); QUAY CO.: Tucumcari Field Station, *Burnham* s.n. (US); ROOSEVELT CO.: 2 miles S of Portales, *Turner* 4720 (TEX). **Oklahoma:** CADDO CO.: 4 miles W of Anadarko, Hopkins, *Nelson & Nelson* 881 (MO); MC CLAIN CO.: Johnson's pasture, *Barkley* 1499 (MO). **Wyoming:** CONVERSE CO.: T. 38

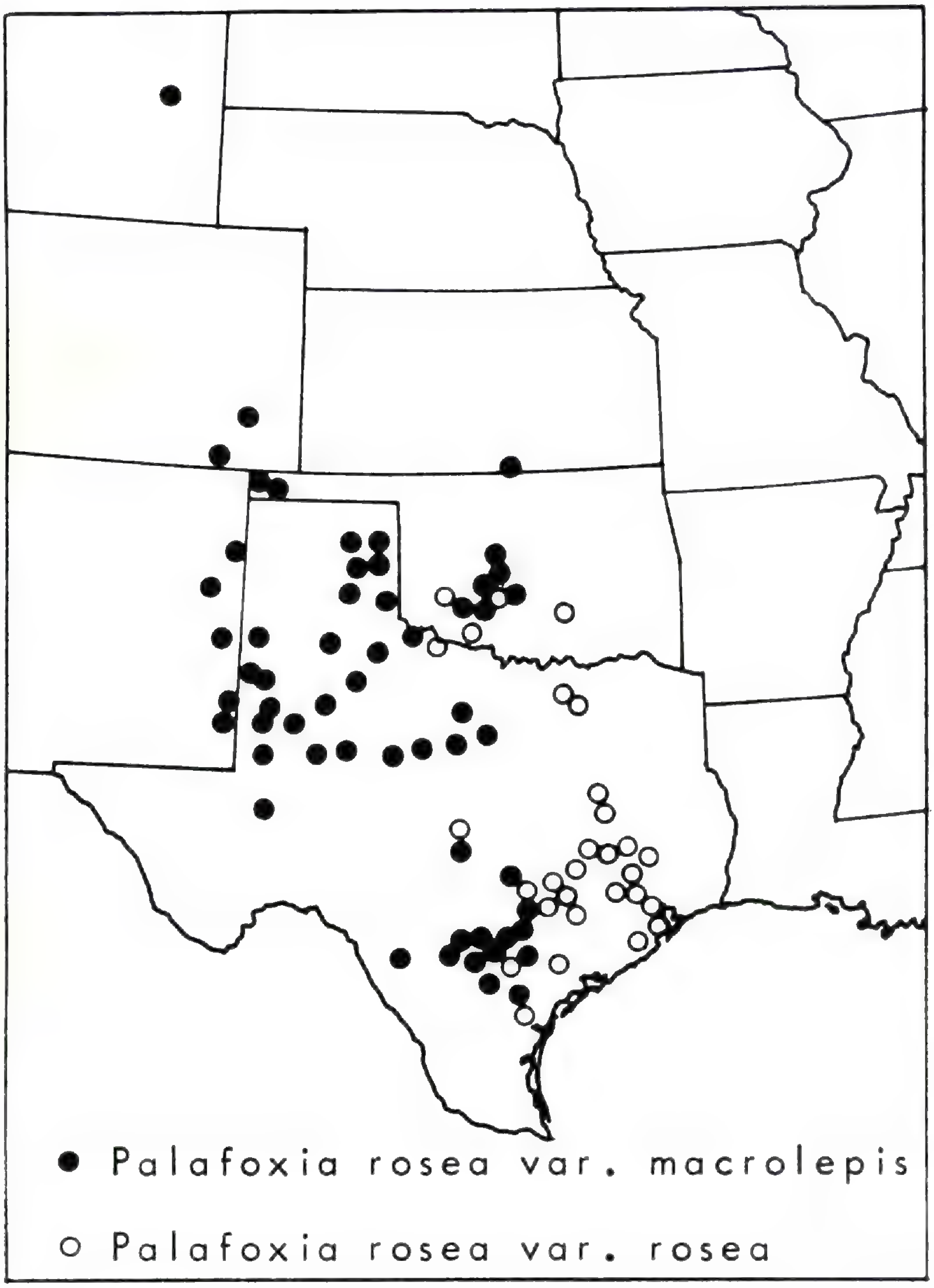

Fig. 21. Distribution of *Palafoxia rosea* var. *rosea* and *P. rosea* var. *macrolepis*.

N., R. 67 W., *Ownbey* 1051 (GH, MO, NY, UC). **Texas:** ANDREWS CO.: 1 mile S of Andrews, *Gentry* 1919 (ARIZ); ATASCOSA CO.: Pleasanton, *Palmer* 9757 (DS, US); BEE CO.: Papalote, *Albers* 46338 (TEX); BEXAR CO.: S of San Antonio, *Ammerman* 97 (MO, UC); CALLAHAN CO.: Clyde, *Palmer* 13818 (US); COCHRAN CO.: Whiteface, *Turner* 4718 (TEX); CRANE CO.: 4 miles S of Crane, *Tharp* s.n. (GH, TEX); DAWSON CO.: 8 miles N of Lamesa, *Rose-Innes & Moon* 1062 (TEX); DEWITT CO.: western part of county, *Riedel* s.n. (TEX); DICKENS CO.: Spur, *Reed* 3240 (US); DONLEY CO.: 10 miles NW of Clarendon, *Rose-Innes & Moon* 1022 (TEX); EASTLAND CO.: Ranger, *Hodge Oak School* s.n. (UC); ECTOR CO.: 8 miles S of Odessa, *Tharp* s.n. (TEX, US); FLOYD CO.: escarpment of Staked Plains, *Ferris & Duncan* 3375 (CAS, DS, MO); GARZA CO.: 10 miles from Post City, *Ruth* 1246 (MICH); GONZALES CO.: *Whitehouse* s.n. (MICH, TEX); HARDEMAN CO.: Chillicothe, *Ball* 979 (US); HOWARD CO.: Big Springs, *Tracy* 7882 (F, GH, TEX, US); KARNES CO.: Karnes City, *Johnson* 827 (TEX); LIVE OAK CO.: 11 miles N of Three Rivers, *Thompson & Turner* 12 (TEX); LLANO CO.: Field Creek, *Turner & Johnston* 2512 (TEX); MITCHELL CO.: Colorado City, *Oyster* s.n. (CAS, MICH); HEMPHILL CO.: 2 miles NE of Canadian, *Cory* 16272 (GH); TERRY CO.: Wellman, *Reed* 3788 (TEX, US); TRAVIS CO.: Austin, *Tharp* 189 (MO, TEX); WILSON CO.: 10 miles SW of Floresville, *Sullivan & Turner* 1 (TEX).

Baltzer (1944) recognized this taxon as a variety of *Palafoxia texana* as did Shinners (1952), although the former worker restricted the name to plants from Colorado and Wyoming, designating the Texas and Oklahoma material as variety *texana*. We agree with Shinners that the Texas populations belong with var. *macrolepis*, but differ with his placement of the variety in *P. texana*. Rydberg (1910) also suggested that the relationship of var. *macrolepis* is with *P. rosea* but preferred to confer specific status.

The two varieties of *Palafoxia rosea*, as treated here, both having chromosome numbers of $n = 10$, intergrade over a broad region from east to west, and occupy sandy soils. After years of observations on numerous populations, we conclude that they are indeed more closely related to each other than either is to any other taxon. *Palafoxia texana* is composed of 3 varieties, all diploid with $n = 11$; these taxa replace each other geographically and intergrade peripherally. To the north *P. texana* is replaced by the contiguous *P. rosea*.

12. **Palafoxia texana** DC. Prodr. 5:125. 1836. TYPE: UNITED STATES. **Texas:** Berlandier pl. exs. 2014 (Photograph of holotype, G-DC!; isotypes, GH!, MO!).

12a. **Palafoxia texana** DC. var. **texana.** Fig. 22.

Polypteris texana (DC) Gray, Proc. Am. Acad. 19:30. 1883. *Othake texanum* (DC.) Bush, Trans. Acad. Sci. St. Louis 14:176. 1904.

Othake canescens Rydb., N. Am. Fl. 34:60. 1914. TYPE: MEXICO. **Nuevo Leon:** Monterey, *Pringle* 1919 (Holotype, NY!; isotypes, F!, MICH!, UC!, US!).

Plants annual, 20-80 cm tall; stems erect, usually several from a suffruticose base (often appearing perennial), densely pubescent with white, scabrous, appressed hairs, capitate glandular only in the inflorescence; mid-stem leaves linear-lanceolate to ovate-lanceolate, 3-nerved, 0.5-2.0 cm wide, 3-8 cm long, with petioles 1-3 cm long; principal involucral bracts 12-15, linear-oblanceolate, acute to obtuse, densely strigose, not or rarely glandular; florets pinkish-white to pink, regular; corolla 8-10 mm long, tube slender, 3.5-5.0 mm long, throat campanulate, 0.4-0.6 mm long, lobes linear, 3-4 mm long; style branches 3-5 mm long; achenes 4-6 mm long, obpyramidal, 4-sided, rather evenly pubescent with short, silky, ascending hairs; pappus scales 8, 2.5-5.0(-6) mm long (the outermost achenes with the shorter scales); chromosome number, $n = 11$.

Distribution: Southern Texas and adjacent Mexico, mostly in rocky or gravelly calcareous soils. Flowering, Mar.-Nov. depending on rains. Fig. 18.

REPRESENTATIVE SPECIMENS. UNITED STATES. Texas: DIMMIT CO.: Carrizo Springs, *Palmer* 33725 (MO, US); DUVAL CO.: 9 miles N of Freer, *Thompson & Turner* 35 (TEX); FRIO CO.: Melon, *Muller* 2608 (MICH, UC); HIDALGO CO.: 1 mile N of Tabasco, *Clover* 93 (ARIZ); KINNEY CO.: "river highway" 1 mile N of Maverick County line, *Johnston* 3879 (TEX); LA SALLE CO.: 1 mile E of Cotulla, *Ferris & Duncan* 3041 (CAS, DS, MO); MC MULLEN CO.: 2.5 miles S of Tilden, *Tharp & Johnston* 541776 (TEX); MAVERICK CO.: 6 miles N of

Fig. 22. *Palafoxia texana* var. *texana*. A. Whole plant, ×¼. B. Head, ×2½.

Quemado, *Johnston* 3861 (TEX); MEDINA CO.: 2 miles SW of Devine, *Turner* 4561 (TEX); STARR CO.: about 5 miles SE of Rio Grande City, *Correll* 14894 (US); UVALDE CO.: 7 miles SW of Uvalde, *Shinners* 7371 (GH, UC); VAL VERDE CO.: Del Rio, *Jones* 26398 (DS, MO, US); WEBB CO.: near Laredo, *Mackenzie* 7 (ARIZ, MICH, MO); ZAPATA CO.: Highway 83, *Parks* RX 2884 (MO).

MEXICO. **Coahuila:** between Hipolito and Sacramento in El Desierto de la Playa, *Wynd & Mueller* 83 (ARIZ, GH, US); San Lazaro near the northern entrance of El Puerto de San Lazaro, *Wynd & Muller* 120 (ARIZ, GH, US); 23 miles SW of Monterey, *Warnock & Barkley* 14878M (F, TEX); 90 miles N of Saltillo, *Turner*

3981 (TEX); 20 miles N of Monclova, *Turner* 3984 (TEX); 8 miles SW of Saltillo, *Shreve* 8730, (ARIZ, MICH, US); La Rosa, W of Saltillo, *Shreve & Tinkham* 9589 (GH, MICH, UC); La Fariba cerra de Nuevo Laredo, *Selar* 1031 (GH); about 30 km ESE of Cuatro Cienegas, *Schroeder* 164 (GH); Soledad, Sabinas, *Nelson* 6772 (US); Muzquiz, *Marsh* 1124 (F, GH, TEX); Hermanas, about 40 km northeasterly from Monclova, *Marsh* 1616 (F, GH, TEX); Monclova, *Marsh* 1730 (F, GH, TEX); 15 miles SE of Sabinas on the road to Don Martin, *Johnston* 4335 (TEX); 8 miles W of Saltillo, *Johnston* 7665 (GH); Canon de la Charretera, Sierra de la Madera, *Johnston* 9171 (GH); 6 km E of Saltillo, *Hinton* 16873 (GH). **Nuevo Leon:** 14 km S of Nuevo Laredo, *Frye & Frye* 2385 (DS, GH, MO, UC, US); 12 miles N of Sabinas Hidalgo, *Heard & Barkley* 14546 (GH, TEX, US); 16 miles SW of Villa Santa Catarina, *Hernandez, Roswell, Jr. & Barkley* 16M514 (TEX); 27 miles W of Monterey, *Johnston & Graham* 4318 (TEX); Monterey, *Pringle* 1919 (F, MICH, UC). **Puebla:** w/o locality, *Nicolas* s.n. (F). **Tamaulipas:** 10 miles S of Nuevo Laredo, *Heard & Barkley* 14583 (TEX, US); near Dolores (24° 00′ × 97° 55′), *Crutchfield & Johnston* 5048 (TEX); 3 miles W of Morales, *Crutchfield & Johnston* 5351 (TEX).

Palafoxia texana var. *texana* apparently grades into var. *ambigua* along the eastern portion of its range (*Tharp & Johnston* 541776, TEX; *Thompson & Turner* 35, TEX; *Graham & Johnston* 4367, TEX).

Shinners (1952) treated the *macrolepis* segregate as a variety of this species but on cytological, morphological and geographical grounds the former appears to be better treated as a variety of *Palafoxia rosea.* For the same reasons *P. rosea* var. *ambigua* of Shinners appears to be best treated as a variety of *P. texana.*

12b. **Palafoxia texana** var. **ambigua** (Shinners) B. L. Turner & M. I. Morris, comb. nov. Fig. 23.

Palafoxia rosea var. *ambigua* Shinners, Field & Lab. **20:** 95. 1952. TYPE: UNITED STATES. **Texas:** SAN PATRICIO CO.: Aransas Pass, *Cory* 51241 (Holotype, SMU!; isotypes, DS!, GH!).

Resembling var. *texana* except in being less branched at the base, and possessing longer leaves, shorter pappus scales, narrower and mostly eglandular involucral bracts; chromosome number, $n = 11$.

Distribution: Southernmost Texas and adjacent Mexico, mostly in sandy or silty-sandy soils. Flowering, Feb.-Nov., depending on rains. Fig. 18.

REPRESENTATIVE SPECIMENS. UNITED STATES. **Texas:** ARANSAS CO.: Rockport, *Fisher* 39091 (ARIZ, CAS, TEX, US); BEE CO.: Highway 181, *Parks* s.n. (MO); BEXAR CO.: Highway 181, *Parks* s.n. (MO); BROOKS CO.: 12.1 miles SE of Hebbronville, *Cory* 16943 (GH); CAMERON CO.: Rio Hondo, *Chandler* 7035 (GH, UC, US); CALHOUN CO.: Magnolia Beach, *Turner* 4332 (TEX); DUVAL CO.: 17¾ miles N of Freer, *Cory* 55315 (US); HIDALGO CO.: Edinburg, *Fisher* 41060 (CAS, US); JACKSON CO.: S of Vanderbilt, *Tharp & Barkley* 13A156 (DS, TEX); JIM HOGG CO.: Peira Station, *Harvard* s.n. (US); JIM WELLS CO.: 2 miles S of Premont, *Ferris & Duncan* 3246 (CAS, DS); KARNES CO.: 2.4 miles NNE of Runge, *Johnston* 971 (TEX); KENEDY CO.: El Toro Island, *Tharp* 49120 (TEX, US); KLEBERG CO.: Riviera, *Tharp* 3876 (TEX, US); MC MULLEN CO.: 15 miles N of Freer, *Thompson & Graham* 78 (TEX); NUECES CO.: Corpus Christi Bay, *Heller* 1562 (ARIZ, GH, MICH, MO, UC, US); REFUGIO CO.: Highway 35, *Parks* s.n. (MO); SAN PATRICIO CO.: Aransas Pass, *Cory* 51241 (DS, GH); STARR CO.: 3 miles W of Sullivan City, *Lundell & Lundell* 9884 (ARIZ, DS, MICH, US); VICTORIA CO.: Highway 77, *Parks* s.n. (MO); WILLACY CO.: near Redfish Bay, *Lundell & Lundell* 8774 (GH, MICH); WILSON CO.: w/o locality, *Parks* s.n. (MO); ZAPATA CO.: San Ygnacio, *Tharp* 3880 (TEX, UC).

MEXICO. **Tamaulipas:** de Matamoras a San Fernando, *Berlandier* 3027 (GH, MO); 34 miles S of Matamoros, *Crutchfield & Johnston* 5484 (TEX); south of Rio Tigre crossing, *LeSueur* 482 (F, TEX); Morales, *LeSueur* 483 (ARIZ, F, TEX).

Shinners (1952) treated this taxon as a variety of *Palafoxia rosea* apparently because it usually possesses eglandular involucral bracts, a technical feature which he used to distinguish between the species *P. rosea* and *P. texana*. Occasional specimens of *P. texana* var. *ambigua* are found with conspicuous glandular bracts (e.g. *Warnock* 21002, TEX) and many specimens may be found with only a few scattered glandular trichomes. Likewise, specimens similar to var. *texana* are often found with eglandular bracts. On total morphological grounds, chromosome number, distribution, and because it grades into *P. texana* to the west, we have treated the taxon as a variety of that species.

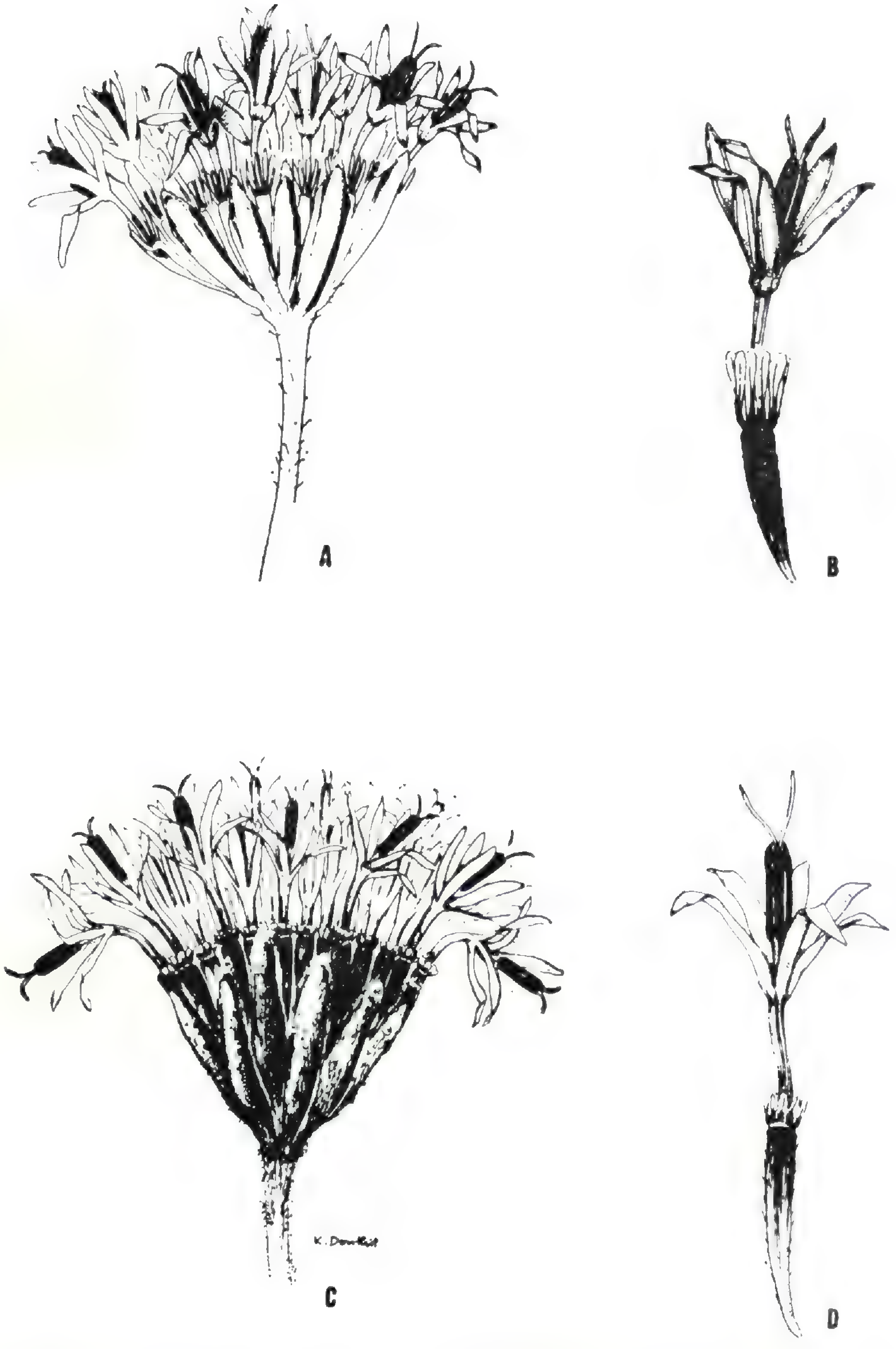

Fig. 23. *Palafoxia texana* var. *ambigua*, A & B. *P. texana* var. *robusta*, C & D. A. Head, ×2½. B. Floret, ×3. C. Head, ×2½. D. Floret, ×4.

12c. **Palafoxia texana** var. **robusta** (Rydb.) B. L. Turner & M. I. Morris, comb. nov. Fig. 23.

Othake robustum Rydb., N. Am. Fl. 34:60. 1914. TYPE: MEXICO. **Tamaulipas:** sand dunes of Gulf Coast, Tampico, *Pringle* 6354 (Holotype, NY!; isotypes, CAS!, F!, MO!, UC!). *Polypteris robustum* (Rydb.) Cory, Rhodora 38:408. 1936. *Othake roseum* var. *robustum* (Rydb.) Ammerman, Ann. Mo. Bot. Gard. 31:257. 1944.

Much resembling *P. texana* var. *ambigua* but differing from that taxon in being much more robust (mostly 0.9-2.1 m tall), with larger heads and longer achenes (6-7 mm); chromosome number not determined.

Distribution: Dune sands along the Gulf Coast from northernmost Veracruz to central Tamaulipas. Flowering, Jul.-Nov. or later, depending on rains. Fig. 18.

REPRESENTATIVE SPECIMENS. MEXICO. **Tamaulipas:** Tampico, *Fisher* 46177 (CAS, US); Tampico, *Kenoyer* 728 (F, MO); 1 mile N of Ciudad Madero, *King* 4003 (TEX); 2 miles NE of Altamira, *King* 4030 (TEX); Tampico, Miramar, *Mell* s.n. (NY); vicinity of Tampico, *Palmer* 38 (CAS, F, GH, MO, NY, US); 8 miles NE of Tampico, *Waterfall & Wallis* 14642 (F). **Veracruz:** 1 miles N of Las Casitas (across the river from Nautla), *Graham & Johnston* 4803 (TEX); 2 kilometers out of Tampico on road to Valles, *Johnston* 4055A (TEX); La Guadalupe (20° 25′ N.L.), ca. 15 kilometers S of Rio Tecolutla mouth, *Sauer & Gade* 3022 (WIS).

EXCLUDED NAMES

Palafoxia pedata (Cav.) Shinners, Field & Lab. 17:25. 1949. This name refers to *Florestina pedata* (Cav.) Cass. Dict. Sci. Nat. 17:155. 1820.

Palafoxia liebmannii (Schz. Bip. ex Greenm.) Shinners, Field & Lab. 17:25. 1949. This name refers to *Florestina liebmannii* Schz. Bip. ex Greenm. Field Mus. Publ. Bot. 2: 272. 1907.

Palafoxia tripteris (DC.) Shinners, Field & Lab. 17:24. 1949. This name refers to *Florestina tripteris* DC. Prod. 5:655. 1836.

ACKNOWLEDGMENTS

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LITERATURE CITED

BALTZER, E. A. 1944. A monographic study of the genus *Palafoxia* and its immediate allies. Ann. Mo. Bot. Gard. **31**:249-278.

BENTHAM, G., & J. D. HOOKER. 1873. *In:* Genera plantarum **2**:405.

BLAKE, S. F. 1945. Asteraceae described from Mexico and the southwestern United States by M. E. Jones, 1908-1935. Contr. U.S. Nat. Herb. **29**:117-137.

BUSH, B. F. 1904. The genus *Othake* Raf. Trans. Acad. Sci. St. Louis **14**:171-180.

CASSINI, A. DE. 1818. *In:* Bulletin de la societe philomathique de Paris. **1818**:47.

CAVANILLES, A. J. 1794. *In:* Icones et descriptiones plantarum **3**:3, t. 205.

————. 1797. *In:* Icones et descriptiones plantarum **4**:32.

CORY, V. L. 1946. The genus *Palafoxia* in Texas. Rhodora **48**: 84-86.

GRAY, A. 1884. *Florestina, Polypteris, Palafoxia. In:* Syn. Fl. N. Am. 1 pt. **2**:336-338.

HOFFMANN, O. 1894. Compositae. *In:* Engl. & Prantl, Die natürlichen Pflanzenfamilien IV, Abt. **5**:261.

HOOKER, W. J. 1837. *In:* Icones plantarum **2**:148.

JONES, M. E. 1933. *Palafoxia linearis* var. *gigantea. In:* Contr. West. Bot. **18**:79.

LAGASCA, M. 1816. *In:* Elenchus plantarum hort. matr. 26 & Genera et species nov. 26.

NELSON, A. 1936. Rocky Mountain Herbarium studies. IV. Am. J. Bot. **23**:265-271.

NUTTALL, T. 1818. *In:* Gen. N. Am. Pl. **2**:139.

RAFINESQUE, C. S. 1836. *Othake. In:* New Fl. Am. **4**:73.

RYDBERG, P. A. 1910. *Othake. In:* Studies on the Rocky Mountain flora — XXII. Bull. Torr. Bot. Club **37**:330-332.

————. 1914. *Polypteris. In:* N. Am. Fl. 34 pt. **1**:61-62.

SHINNERS, L. H. 1949. Notes on Texas Compositae — I. Field & Lab. **17**:23-30.

————. 1952. The Texas species of *Palafoxia* (Compositae). Field & Lab. **20**:92-102.

Turner, B. L. 1963. Taxonomy of *Florestina* (Helenieae: Compositae). Brittonia 15:27-46.

———, & A. M. Powell. 1977. Disposition of genera in the dismantled polyphyletic tribe Helenieae (Asteraceae). *In:* The Biology and Chemistry of the Asteraceae. Eds. Heywood, Harborne and Turner. Academic Press: (In press).

———, & M. I. Morris. 1975. New taxa of *Palafoxia* (Asteraceae: Helenieae). Madrono 23:79-80.

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CHROMOSOMES OF MEXICAN SEDUM
I. ANNUAL AND BIENNIAL SPECIES

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Probably well over 100 species of *Sedum* are native to Mexico. Jacobsen (1974), whose concept of the genus is followed most closely here, listed 82 species for Mexico, but several of these probably are best reduced to synonymy. On the other hand, Jacobsen omitted some species that appear distinct, and new species are still being found at a significant rate as new areas become accessible. At least ten species of *Sedum* studied for this series of papers are considered to be new and undescribed.

Sedum is the catchall genus for the Crassulaceae, and in addition to the more "typical" species it includes a number of peculiar species that are not easily assigned to other named genera. In vegetative habit the Mexican sedums range from annuals and biennials to mostly perennials, and from delicate, minute herbs to plants that are creeping or pendulous or with sessile rosettes to bushes 2 meters or more high. With a few exceptions the floral form is reasonably constant, with 5 sepals, 5 essentially separate and spreading petals, ten stamens in two whorls, and 5 separate carpels. However, one (unnamed) biennial species is tetramerous (Fig. 19), and in other species some flowers are 6 or more parted. In some species the corolla is mostly or partly erect, spreading only in the distal half or less, and in a few species the petals are basally connate for as much as 1 or 2 mm. Two species (one of them undescribed) have only 5 stamens. In a few species the nectar scales are greatly enlarged (e.g., Fig. 19), and a few have the carpels united for a short distance at the base. Most species form inflorescences at the tips of previously vegetative stems, but some species (Section *Pachysedum*) regularly bear lateral inflorescences.

Important characters of succulent plants are not well preserved in herbarium specimens, which therefore may

provide seriously inadequate information when new species are described from them. This deficiency is compounded when the type locality is not clearly indicated or cannot be located today. Thus, identification of some plants is very difficult because descriptions of some species are inadequate, having been based on dried specimens.

In these studies about 50 different chromosome numbers ranging from $n = 7$ to $n =$ ca. 140 have been found in the 90 or so species studied. Generally a rather broad concept of species has been followed, and some species, as conceived here, are variable morphologically. A good many are also variable cytologically, with two or more chromosome numbers, and one species has no less than ten numbers.

Most collections came from known localities in the wild, but many were grown in the greenhouse before study. Pressed vouchers of virtually all are in the Wiegand Herbarium or Bailey Hortorium of Cornell University. Chromosomes were studied at meiosis in conventional acetocarmine squashes of pollen mother cells. Photographs (all $\times$ 2,000) are of permanent preparations.

I am particularly indebted to Dr. Reid Moran, Natural History Museum, San Diego, California, who has collected and identified many specimens. Other collections were generously provided by my colleague Professor R. T. Clausen, by Paul C. Hutchison, then of the Botanical Garden, University of California, Berkeley, and by Myron Kimnach of the Huntington Botanical Garden, San Marino, California.

For reasons of logistics and economics these counts are reported in a series of papers, rather than all in one. This first paper reports on the chromosomes of only the annual and biennial species, which are themselves rather diverse in form and chromosome number, and obviously include some species that are not closely related. Some of these species are not well known and some identifications are very uncertain. At least one is new. Still other annual and biennial species have not been available for study. I hope that the reports of the chromosome numbers here, together

with the locality data, may contribute to an eventual clarification of this poorly understood group.

The biennials usually die to the ground during the dry season (winter and spring), then look very different the second year, especially in their leaves. All biennial species have proved difficult to grow in cultivation, and this has limited direct comparison of living plants. In most cases their names and published descriptions have been based on pressed material. The authors of the species had never seen the living plants and seem not to have known whether they were annual, biennial or perennial. (Indeed, some individual plants may vary in this respect.) Jacobsen (1974) listed eight of the species reported here, three, apparently based on published descriptions, as perennials: *S. chihuahuense* (as *Villadia*), *S. flaccidum,* and *S. napiferum.* Five others were described as annual or biennial: *S. batesii* (as *Villadia hemsleyana*), *S. cormiferum, S. forreri, S. jaliscanum,* and *S. minimum.*

The species studied and their chromosome numbers are listed alphabetically in Table I; under each species collections are arranged from north to south and from west to east. The species are discussed below in geographic order, from north to south.

Table I. Collections Studied.

Sedum cf. *batesii* Hemsley $n = 31$

M10106 Oaxaca. 3 mi NW of Lachao at km 177 on road to Puerto Escondido, 1850 m (R. Moran) (Fig. 1).

Sedum cf. *chihuahuense,* Wats.

U2254 Durango. 4.5 km W of Revolcaderos, 2075 m ($n = 10$).

U2253F_1 Durango. 3 km W of Revolcaderos, 2100 m ($n = 10$).

U1657 Durango. 9 km W of Espinazo, Mex. hwy. 40. (W. Handlos 469A) (two plants both $n = 9$, Fig. 2).

U1385 Durango. 4.4 km W of Espinazo monument, Mex. hwy. 40, 2300 m ($n = 10$, Fig. 3).

Sedum cormiferum Clausen $n = 14$

SV-VG102a State of Mexico. Ravine tributary to gorge of Tenancingo R., 4 km SSE of Villa Guerrero (R. T. Clausen, from the type collection) (Fig. 4).

Sedum cf. *flaccidum* Rose $n = 11$

U1377 Durango. Wet flattish rocks 5 km E of La Ciudad, 2600 m (Fig. 5).

U1660 Durango. 8.5 km E of La Ciudad (W. Handlos 471A).

Sedum cf. *forreri* Greene $n = 8$

U1384 Durango. 12.6 km W of La Ciudad.

U1658 Durango. 11 km W of La Ciudad (W. Handlos) (Fig. 20).

M9995 Durango. La Ciudad, 2700 m (R. Moran) (Fig. 6).

U1376 Durango. 7.3 km W of El Salto.

M13332 Durango. 8 km S of El Salto, 2550 m.

U1540 Durango. Just E of Navajas, ca. 65 km W of Durango.

M13322 Durango. Navios, 59 km W of Durango, 2300 m (R. Moran).

U1374 Durango. Mex. hwy. 40 at km 55 marker W of Durango city, 1.9 km W of Tepalcates, 2550 m.

Sedum jaliscanum S. Wats.

U1396 Zacatecas. Juchipila Canyon, 7 km S of Moyahua, km 99 N of Guadalajara, 1100 m ($n = 18$).

U1400 Jalisco. 5.5 km E of Ayo el Chico. ($n = 24$ prob).

U2142 Jalisco. In barranca at km 18 N of Guadalajara, 1300 m (probable topotype). ($n = 18$, Fig. 9).

U2114 Guanajuato. Picachos de la Bufa, NE of Guanajuato city, 2300 m ($n = 18$).

U2259 Michoacán. 7 km W of Zacapu, 2200 m, on lava. ($n = 11$, Fig. 7).

U2137 Michoacán. Km 49 on Pátzcuaro road, 14 km E of Uruapan, on lava. ($n = 34$, Fig. 14).
U1405 Michoacán. Mex. 37 at km 94, 19 km S of Uruapan, 1280 m ($n = 34$).
U1415 Michoacán. Sierra de Ozumatlan, 32 km E of Morelia. ($n = 20$, Fig. 10).
U2266 Michoacán. 7.5 km S of Zinapécuaro, 2080 m ($n = 23$, Fig. 12).
U2264 Michoacán. 1 km N of Huajúmbaro, 2250 m ($n = 25$, Fig. 13).
U2262 Michoacán. 3.2 km SE of Huajúmbaro, 2380 m ($n = 25$).
U1426 State of Mexico. Below Presa Tilostoc, S of Valle de Bravo ($n = 17 \pm 1$).
U1737 State of Mexico. Barranca de Ahuatenca. (R. Moran). ($n = 20$).
U1445 Guerrero. Taxco. ($n = 16$, Fig. 8).
SV-T17 Guerrero. N Side of Taxco (R. T. Clausen). ($n = 16$).
U1434 Morelos. 1.5 km W of Tepoztlán. (Topotype of *S. naviculare* Rose). ($n = 21$, Fig. 11).

Sedum minimum Rose $n = 11$
U1470 Hidalgo. Meadow in fir forest, 2 km N of Pueblo Nuevo, El Chico Natl. Park, 3000 m (Fig. 15).

Sedum napiferum Peyritsch $n = 11$
U1422 State of Mexico. Flattish rocks on W spur of hill N of Toluca, 2750 m (Fig. 16).
#5 Same locality (R. T. Clausen).

S. cf. *vinicolor* S. Wats. $n = 7$
M21964 Sonora. 6 km NW of Yécora, 1525 m (R. Moran) (Fig. 17).

S. sp. $n = 22$
U1381 Durango. Puerto Buenos Aires, 9 km W of La Ciudad, 2700 m.
U1659 Same locality (W. Handlos) (Fig. 18, 19).

The northernmost collection, *Sedum* cf. *vinicolor* S. Wats., is a fibrous-rooted annual about 10 cm high, much branched at and near the base, with stems and leaves marked with many tiny wine-colored spots, probably depending partly on exposure to sun. The sepals are green, rather thick and spreading, a little shorter than the corolla. The petals are pale greenish yellow in the distal half, increasingly marked toward the base with wine-colored spots, usually in transverse bands. The filaments and pistils are heavily spotted with the same color. The plants resemble *S.* cf. *forreri* from farther south, but the petals are narrower and yellowish in background color (vs. white in cf. *forreri*), and the carpels do not become as widely spreading. This species has the lowest chromosome number ($n = 7$, Fig. 17) yet found in more than 200 species of Mexican Crassulaceae studied (Uhl, 1970; Uhl and Moran, 1973; Uhl, unpublished). The plant came from near Yécora, Sonora, near the Chihuahua border and probably less than 100 km from the type locality of *S. vinicolor* (Norogachi, Chihuahua) but more than 1000 meters lower.

The next four species were collected along or near the highway (Mex. 40) from Durango to Mazatlan, which provides the only good access to the vast Sierra Madre Occidental. The genus is very poorly known in this area, and the identifications from here also are only tentative.

Sedum sp., a small napiform biennial with very pale greenish tetramerous flowers and conspicuous brownish nectaries (Fig. 19), is very distinctive and certainly an undescribed species ($n = 22$, Fig. 18). It was found only at Puerto Buenos Aires, 9 km west of the sawmill town of La Ciudad and 154 km west of Durango city.

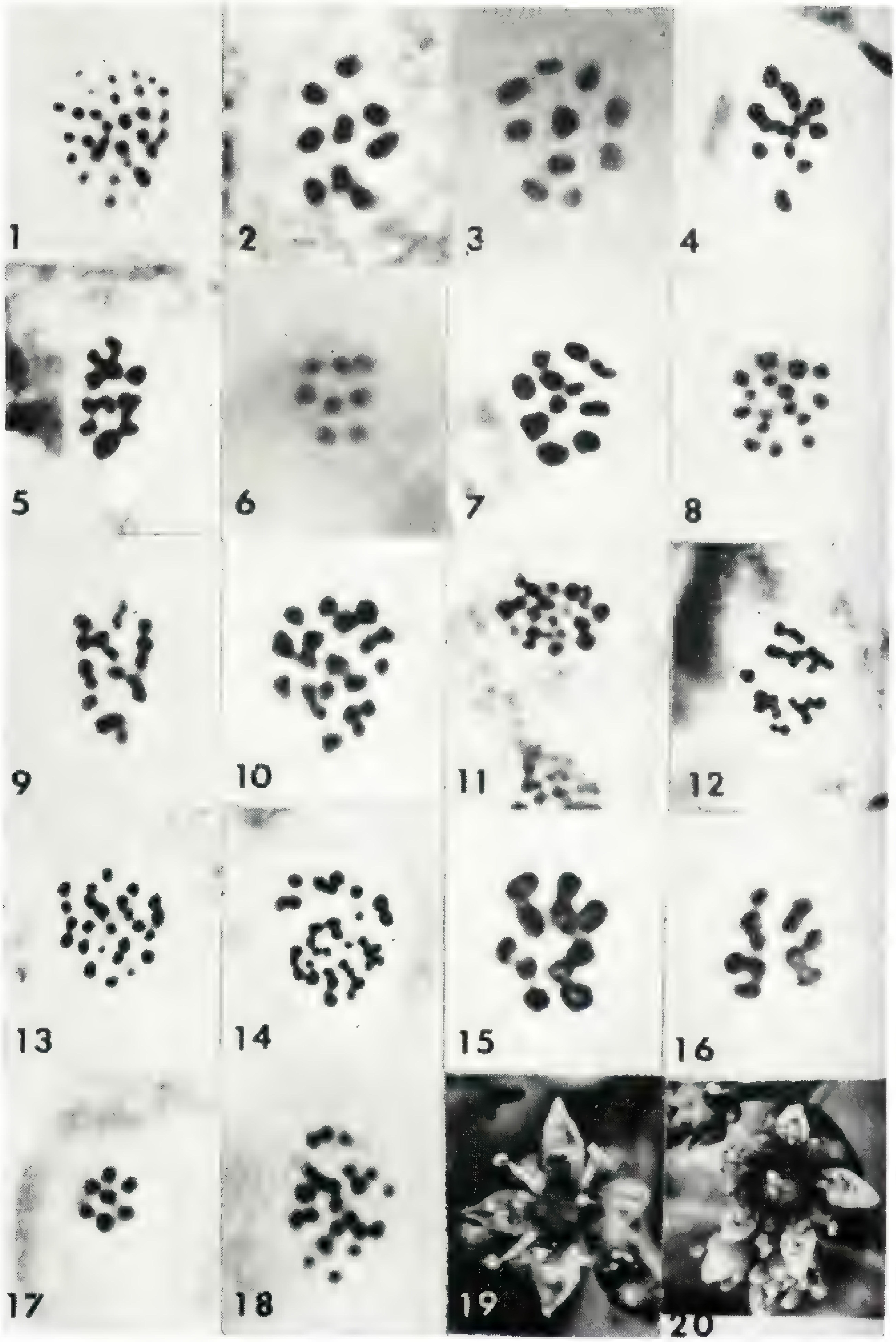
Sedum cf. *forreri* Greene is a fibrous-rooted annual with leaves and stems usually strongly flushed with red and with white petals cross-banded with red (Fig. 20; $n = 8$, Fig. 6). It occurs at many rocky places along the road from 55 km west of Durango for about 100 kilometers westward, to west of Puerto Buenos Aires. The type locality of *S. forreri* is vaguely given as the "higher Sierra Madre, back

of the city of Durango" at 8100 feet, and the petals are described as white or faint rose color.

Sedum cf. *flaccidum* Rose is a napiform biennial (?) with flowers similar to those of *S.* cf. *forreri* in coloring, found on open, wet, flattish rocks at two places a few kilometers east of La Ciudad. *S. pringlei* S. Wats. is possibly an older name for the same species. The type locality of *S. flaccidum* is Tejamén, Durango, about 135 km NE of La Ciudad, whereas *S. pringlei* was described from Cusihuiriáchic, Chihuahua, more than 500 km to the north. Whatever its name, its morphology, habitat and chromosome number ($n = 11$, Fig. 5) suggest a relationship with *S. napiferum* and *S. minimum* of central Mexico.

Sedum cf. *chihuahuense* S. Wats. ($n = 9$ and 10, Figs. 2, 3), the fourth species of the Durango-Mazatlán road, was found in clefts in steep rock at many places from Espinazo del Diablo (22 km west of La Ciudad) westward for 35 kilometers and into Sinaloa. It is biennial with narrowly oblanceolate leaves the first year, forming a small corm, and the second year producing cymes with small white flowers. This species is quite reminiscent of *S. jaliscanum* of central Mexico, but its first-year leaves are not spatulate.

Sedum jaliscanum S. Wats. is broadly conceived here, following Clausen (1959). It is by far the most widely distributed, occurring in rock crevices often in lava in eight states, from Morelos westward across volcano-studded central Mexico to Nayarit. It is also the most variable of the annual and biennial species studied, both morphologically and cytologically. Clausen found statistically significant differences in 14 of 18 characters among plants from six different localities, but he considered them all the same species. In 16 collections studied at least eight different chromosome numbers were found, ranging from $n = 11$ to $n = 34$ (Fig. 7-14). The type locality is near Guadalajara, where n = 18 was found (U2142, Fig. 9). A topotype of *S. naviculare* Rose, reduced to *S. jaliscanum* by Clausen (1959), had $n = 21$ (U1434, Fig. 11). In most collections, especially those with $n = 34$ (Fig. 14), (but not in those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with $n = 18$) the chromosomes differ substantially in size, a rather unusual condition in *Sedum*.

Sedum jaliscanum is widespread as disjunct populations in a rugged volcanic area that is remarkably variable and that must have experienced frequent and drastic changes in local environments. On the one hand, volcanic activity and fluctuations in available moisture during alternate pluvial and dry periods (presumably coinciding with glacial advances and retreats on the higher summits and farther north) must have repeatedly fragmented, decimated, or exterminated earlier populations of the species. On the other hand, the same changes provided new and favorable habitats elsewhere. Over a long period of time numerous colonizations and recolonizations of newly suitable areas must have occurred. These conditions, together with the short biennial generation time, provided a great many chances for new and different chromosomal types to occur and to become fixed. Stebbins (1974, pp. 158-159) pointed out that great chromosomal diversity is found in many groups of herbaceous plants in pioneer habitats of this sort, and he attributed this probably to "selective pressure for linked gene combinations". The favored combinations are not the same in all populations because differences in the environment may favor different gene linkages and different chromosomal arrangements and number.

Figs. 1-18: Chromosomes at metaphase I in pollen mother cells, ×2000. Fig. 1: *S.* cf. *batesii*, M10106, $n=31$. Fig. 2: *S.* cf. *chihuahuense*, U1657, $n=9$. Fig. 3: *S.* cf. *chihuahuense*, U1385, $n=10$. Fig. 4: *S. cormiferum*, SV-VG102a, $n=14$. Fig. 5: *S.* cf. *flaccidum*, U1377, $n=11$. Fig. 6: *S.* cf. *forreri*, M9995, $n=8$. Figs. 7-14: *S. jaliscanum*. Fig. 7: U2259, $n=11$. Fig. 8: U1445, $n=16$. Fig. 9: U2142, $n=18$. Fig. 10: U1415, $n=20$. Fig. 11: U1434, $n=21$ (metaphase II). Fig. 12: U2266, $n=23$. Fig. 13: U2264, $n=25$. Fig. 14: U2137, $n=34$. Fig. 15: *S.* cf. *minimum*, U1470, $n=11$. Fig. 16: *S. napiferum*, U1422, $n=11$. Fig. 17: *S.* cf. *vinicolor*, M21964, $n=7$. Fig. 18: *S.* sp., U1659, $n=22$. Fig. 19: Flower of *S.* sp. (U1659), ×4. Fig. 20: Flower of *S.* cf. *forreri* (U1658), ×2.5 (millimeter scale).

The highest chromosome number in *S. jaliscanum*, $n = 34$ (Fig. 14), is more than three times the lowest number, $n = 11$ (Fig. 7). However, the size of the chromosomes seems to vary inversely with their number, and the aggregate amount of chromosomal material appears not to differ much. This observation and the presence of so many intermediate numbers suggest that the variation in chromosome number may be sufficiently accounted for by dysploidy, i.e., by evolutionary rearrangement of essentially similar genetic material into different numbers of chromosomes, with no polyploidy involved. Dysploidy is common in the Mexican Crassulaceae, including *Sedum*, but in no other Mexican species has it developed to this extent.

An apparently parallel situation occurs in the similarly polymorphic *S. polytrichoides* of Japan and South Korea, which exhibits a similarly wide range of 13 different chromosome numbers, from $n = 11$ to $n = 35$ (Uhl and Moran, 1972). Calculations of nuclear volume in *S. polytrichoides* showed no correlation with chromosome number, suggesting dysploidy, probably with no polyploidy.

Sedum minimum ($n = 11$, Fig. 15) is known from only three localities, each with perhaps a different subspecies (Clausen, 1959). Stoutamire and Beaman (1960) reported $n = 10$ in *S. minimum* from Nevado de Toluca, the type locality. The material studied here came from Pueblo Nuevo, Hidalgo, a population that Clausen (1959, p. 303-304) considered possibly a different subspecies or even species.

Sedum napiferum ($n = 11$, Fig. 16) is known from only one locality, just north of Toluca. Clausen (1959) considered it closely related to *S. minimum*, and this view is supported by the similarity of their chromosomes. *S.* cf. *flaccidum* (above) occurs in similar habitats (wet, flattish rocks) along the Durango-Mazatlán road. It is similar to these two morphologically; it also has $n = 11$, and it probably is related.

Sedum cormiferum ($n = 14$, Fig. 4) was studied from a plant of the type collection, and its only known locality. Clausen (1959) considered the species most closely related to the perennial *S. clavifolium* ($n = 34$ prob.).

Sedum cf. *batesii* ($n = 31$, Fig. 1) of the Sierra Madre del Sur "is most closely related to *S. jaliscanum*" ($n = 11$ to $n = 34$) of central Mexico (Clausen, 1959, p. 289). Together with *S.* cf. *chihuahuense* ($n = 9$ and 10) of northwestern Mexico, these three may comprise a second group of related biennial species.

Chromosome numbers found in more than 200 species of Mexican Crassulaceae that have been studied include *every* number from $n = 7$ to $n = 36$, as well as many higher numbers (Uhl, 1970; Uhl and Moran, 1973; Uhl, unpublished). It is noteworthy that the three lowest numbers ($n = 7$ to $n = 9$) are known only in the annual and biennial species of *Sedum* reported here, along with several species having $n = 10$ or $n = 11$. The lowest number known in a perennial species is $n = 10$ in an undescribed *Villadia* (Uhl, unpublished).

SUMMARY

Chromosome numbers are reported for ten annual and biennial species, including one undescribed species and several others not certainly identified. *S.* cf. *flaccidum, S. minimum,* and *S. napiferum* are similar morphologically and all have $n = 11$. At least eight different numbers from $n = 11$ to $n = 34$ were found in the widespread and polymorphic *S. jaliscanum,* with the chromosomal variation attributed probably to dysploidy, rather than to polyploidy. *S.* cf. *chihuahuense* ($n = 9$, 10) and *S.* cf. *batesii* ($n = 31$) may be related to *S. jaliscanum. S.* cf. *vinicolor* has $n = 7$, the lowest number known in the Mexican Crassulaceae, and the related *S.* cf. *forreri* has $n = 8$. *Sedum cormiferum* has $n = 14$, and an undescribed species has $n = 22$.

LITERATURE CITED

CLAUSEN, R. T. 1959. *Sedum* of the Trans-Mexican Volcanic Belt. Cornell Univ. Press, Ithaca.

JACOBSEN, H. 1974. Lexicon of Succulent Plants. Blandford, London.

STEBBINS, G. L. 1974. Flowering Plants — Evolution above the Species Level. Harvard Univ. Press, Cambridge.

STOUTAMIRE, W. P. & J. H. BEAMAN. 1960. Chromosome studies of Mexican alpine plants. Brittonia **12**: 226-229.

UHL, C. H. 1970. Chromosomes of *Graptopetalum* and *Thompsonella* (Crassulaceae). Am. Jour. Bot. **57**: 1115-1121.

————, & R. MORAN. 1972. Chromosomes of Crassulaceae from Japan and South Korea. Cytologia **37**: 59-81.

————. 1973. Chromosomes of *Pachyphytum* (Crassulaceae). Am. Jour. Bot. **60**: 648-656.

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EVIDENCE OF NATURAL HYBRIDIZATION BETWEEN MIMULUS RINGENS AND MIMULUS ALATUS (SCROPHULARIACEAE)[1]

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A population of *Mimulus* that consisted of plants typical of *M. ringens* L. and *M. alatus* Ait. as well as plants that exhibited intermediate morphological characteristics was located along the Patapsco River in Baltimore Co., Maryland. A mass collection of the population was made and morphological and chemical studies were initiated to determine whether or not the populational variation was the result of hybridization between the above two taxa.

Mimulus ringens and *M. alatus* are the only representatives of *Mimulus* sect. *Mimulus* (sect. *Eumimulus* of Gray). This section is characterized as a group of erect, glabrous perennials with pinnately veined leaves and leafy racemes. The flowers are usually violet or violet-purple, but occasional white forms are observed. The more common *M. ringens* has clasping or sessile leaf bases, wingless stems, peduncles 3-6 cm. long, and calyx teeth that are usually longer than 2 mm. *Mimulus alatus* has petiolate leaves, winged stems, peduncles less than 1 cm. long, and calyx teeth that are usually shorter than 2 mm.

According to Pennell (1935) the two species are sympatric over most of the eastern United States. He described the habitat of both species as "stream-banks, swales, and swamps, especially where alluvial or calcareous"; however, the authors, while gathering materials of the two species in the Knoxville, Tennessee area, observed that *Mimulus ringens* occurs in open, marshy areas while *M. alatus* occupies shaded stream banks. Whether this generalization holds over the entire range of the two species will require further investigation.

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[1]Contribution from the Botanical Laboratory, The University of Tennessee, Knoxville, N.S. 481.

MATERIALS AND METHODS

Specimens used in this study were collected along the north side of the Patapsco River just west of Gun Road in Baltimore Co., Maryland (*Mimulus ringens* — *Windler* 4083, *M. alatus* — *Windler* 4082 and putative hybrids — *Windler* 4081) and in Knox Co., Tennessee, in open, marshy areas 0.4 mile east of US 129 on the south side of Cherokee Blvd. (*M. ringens* — *Wofford* & *Windler* 5000) and in the woods along a shaded stream bank 4.1 miles south of the Tennessee River on the east side of US 129 (*M. alatus* — *Wofford* & *Windler* 5001). Vouchers are deposited in the University of Tennessee Herbarium, Knoxville (TENN). Although this study centers on the Patapsco River population, specimens from pure populations of *M. ringens* and *M. alatus* from the Knoxville area were examined for purposes of comparison.

The Patapsco River population consisted of approximately fifty individuals of which a very high percentage (ca. 40%) were designated as putative hybrids. Of the remaining plants, ca. 35% were designated as *Mimulus ringens* and ca. 25% as *M. alatus*. The plants were randomly scattered in a partially shaded drainage depression that did not contain water at that time but appeared to collect and retain water for short periods during rains. This could be considered a fairly intermediate habitat between the open, marshy habitat of *M. ringens* and the shaded stream bank habitat of *M. alatus* observed in the Knoxville, Tennessee area.

A scatter diagram of the Patapsco River population (Fig. 1) was constructed in order to obtain a visual representation of the populational variability. Because leaf base shape and winging of the stem are difficult characters to quantify, peduncle length and calyx lobe length were used as the coordinates of the diagram. Measurements were made on flowers at anthesis.

Pollen was obtained from anthers of flowers at anthesis and stained with aniline blue in lactophenol as an indicator

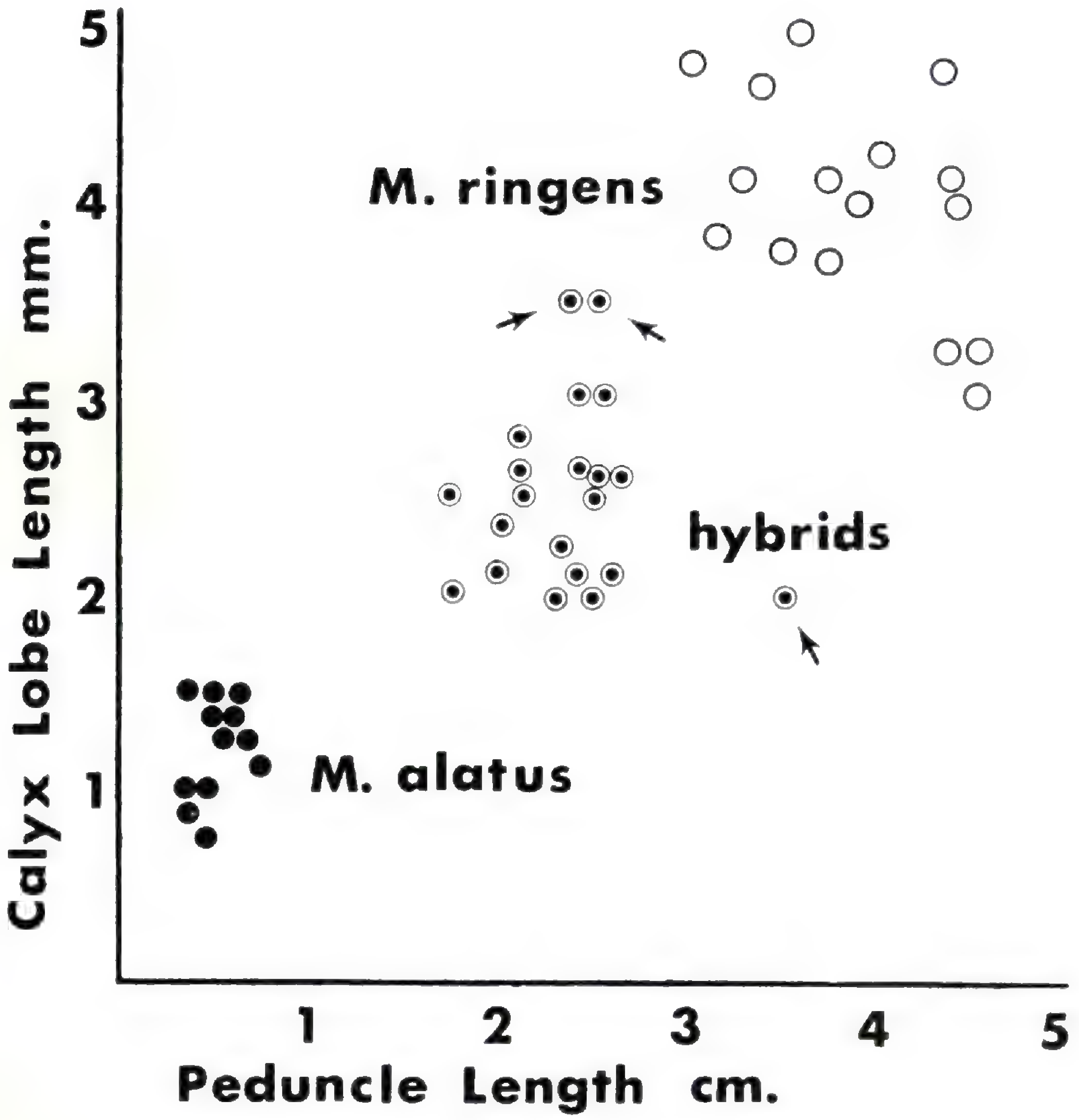

Fig. 1. Scatter diagram of the Patapsco River, Maryland population of *Mimulus*.

of pollen viability. The mean, standard deviation and range were determined for *Mimulus ringens*, *M. alatus*, and putative hybrids from the Patapsco River population and for *M. ringens* and *M. alatus* from pure populations (Table 1). The means were then analysed statistically by the Duncan's new multiple range test modified for unequal numbers of observations (Steel & Torrie, 1960) to determine if there were significant differences in percentages of pollen viability.

All plants used in this study were analysed for flavonoid chemical constituents (Fig. 2, Table 2) following the methods of Mabry, Markham, and Thomas (1970). Midstem leaf material was extracted overnight in 85% methanol, the extract was spotted on Whatman 3MM chromatographic paper and chromatograms were developed in solvent systems of tertiary butanol:glacial acetic acid:water (3:1:1) for the first dimension and 15% glacial acetic acid for the second dimension. When sufficient quantities could be isolated, compounds were analysed by ultraviolet spectroscopy and were hydrolysed by refluxing at 100° C for one hour (3 hours for compound 2) in 6% HCl. Aglycones and sugar residues were separated by partitioning in ethyl acetate and water, the aglycones moving into the ethyl acetate and the sugars into the water. Aglycones were

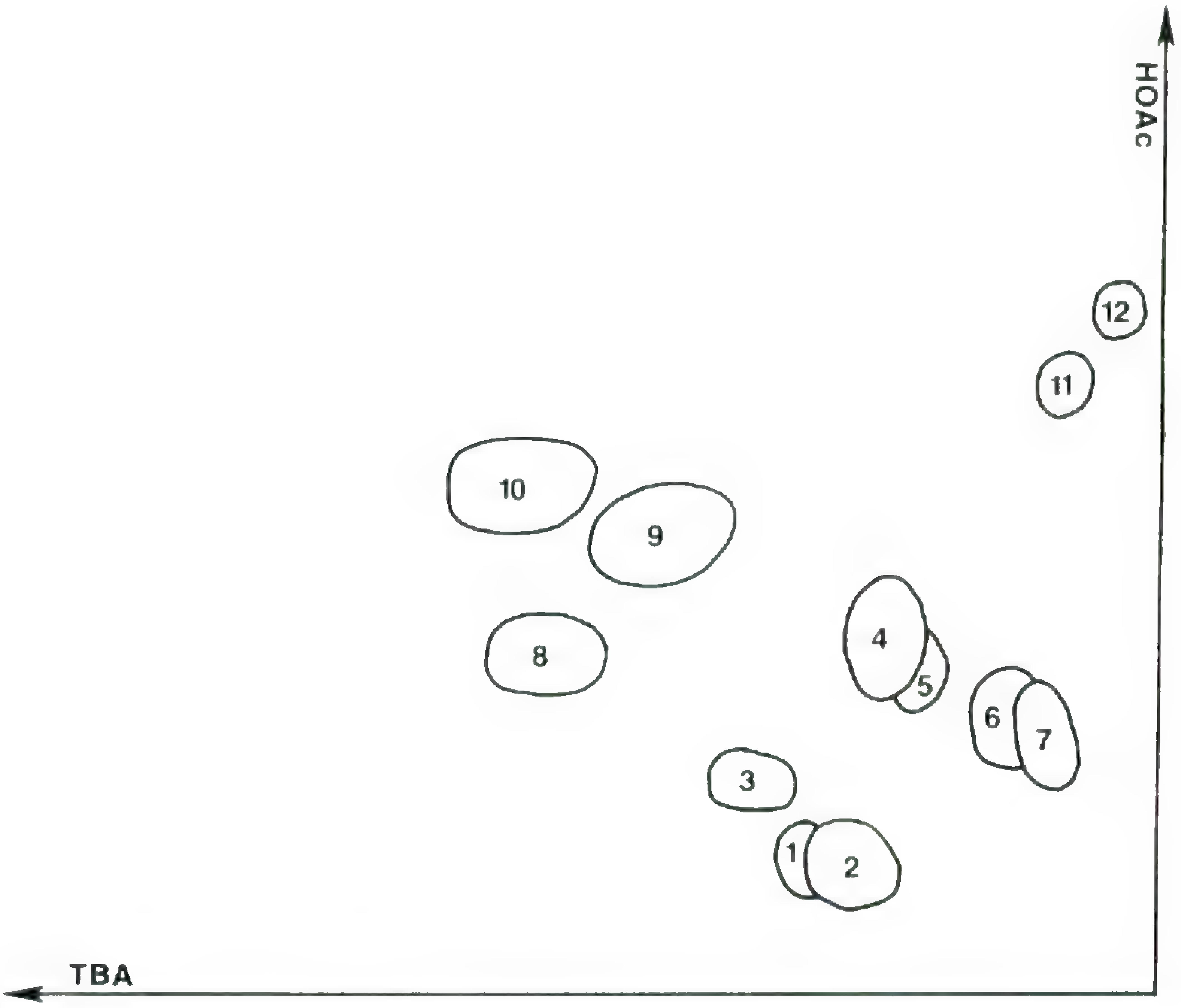

Fig. 2. Composite chromatographic profile of flavonoids in *Mimulus* (Sect. *Mimulus*).

then rechromatographed and analysed by standard procedures. Trimethylsilyl ether derivatives of the sugars were prepared and analysed by comparison to known standards on a Bendix 3600 gas chromatograph equipped with a 6 ft. × 0.25 in. column packed with acid washed silanized chromosorb W coated with 3% SE-52 and run at a temperature of 180° C.

RESULT AND CONCLUSIONS

The scatter diagram (Fig. 1) separates the individuals into three groups. Those at the lower left are most like *Mimulus alatus,* those at the upper right are most like *M. ringens* and those in the center are putative hybrids. The putative hybrids, while fairly closely clustered, exhibit some variability in the direction of the *M. ringens* individuals. This relatively tight clustering would suggest that most are probably F_1 hybrids, but the existence of three individuals somewhat separated from the others (Fig. 1, arrows) could indicate that backcrossing to *M. ringens* has occurred. The variability observed in the *M. ringens* individuals could simply be the result of phenotypic plasticity as is commonly observed in outcrossing species. However, the existence of putative backcross individuals suggests the additional possibility that the morphological variability in *M. ringens* could be the result of introgression. The tight clustering of the *M. alatus* individuals and their clear spacial separation on the diagram from the putative hybrids suggests that there has been little or no backcrossing in the direction of *M. alatus.*

The pollen stainability results are shown in Table 1. The Duncan's new multiple range test showed that pollen stainability in the putative hybrids is significantly lower than that in *Mimulus ringens* and *M. alatus,* but that there are no significant differences among the parental groups tested. If extensive backcrossing (i.e., introgression) were occurring, and assuming that genetic material of one taxon entering the gene pool of another taxon will cause some

Table 1. Pollen Stainability in *Mimulus* (Sect. *Mimulus*)

Taxon	Number of observations	Percent Stainability	St. Dev.	Range
M. alatus (Tenn.)	7	95.71	5.05	85-99
M. alatus (Md.)	10	95.90	4.48	86-100
hybrids (Md.)	16	36.62	8.78	18-49
M. ringens (Md.)	14	94.14	3.99	87-100
M. ringens (Tenn.)	7	97.00	3.26	90-99

meiotic irregularities and hence a higher percentage of inviable pollen, one might expect to observe lower pollen stainability in the parents of the mixed population compared to the parents from pure populations. This does not appear to be an unreasonable assumption in light of the fact that the three individuals indicated on the scatter diagram as possible backcrosses (see also chemical discussion below) have pollen stainabilities of 27%, 34%, and 41% compared to a range of 87-100% among the *M. ringens* individuals. The significantly lower pollen stainability in the putative hybrids, therefore, strongly suggests that hybridization is occurring in the Patapsco River population while no significant differences in pollen stainability among the parental taxa suggest that extensive backcrossing to either parent is not occurring.

A total of 12 phenolic compounds were detected on the chromatograms of the two species and the putative hybrids (Fig. 2). Unfortunately, many of the compounds were very weak and difficult or impossible to identify even after large quantities of leaf material were extracted and chromatographed on columns of Sephadex LH-20. We were unable to obtain any ultraviolet spectral data on compounds 1, 4, 5, 6, 7, and 12, and each of these compounds, therefore, is assumed to be identical in different individuals on

Table 2. Distribution of flavonoids in *Mimulus* (Sect. *Mimulus*)

	Flavonoid											
Taxon	(1)	Luteolin 7-0-glucosylglucuronide (2)	Apigenin 7-0-glycoside (3)	(4)	(5)	(6)	(7)	Quercetin 3-0-glucoside (8)	Quercetin 3-0-rhamnoglucoside (9)	Kaempferol 3-0-rhamnoglucoside (10)	Quercetin 3-0-glycoside (11)	(12)
M. alatus	+	+	+	+	+	+	+	+			+	
hybrids	+	+	+	+	+	+	+	+	+	+	+	+
M. ringens		+	+	+			+	+	+	+		

the basis of Rf values and color characteristics. Spectral data only were obtained for compounds 3 and 11 and they were partially identified as an apigenin 7-0-glycoside and a quercetin 3-0-glycoside, respectively. Spectral data and sugar analyses were obtained for the remaining compounds, which were identified as luteolin 7-0-glucosylglucuronide (2), quercetin 3-0-glucoside (8), quercetin 3-0-rhamnoglucoside (9), and kaempferol 3-0-rhamnoglucoside (10). Of the 12 compounds shown in figure 2, 4 are found

in *Mimulus alatus*, 2 are found in *M. ringens* and 5 are found in both species. All but three of the putative hybrids contain all compounds including one (12) not found in either species (Table 2). This distribution of flavonoids represents a classical case of hybrid complementation in the sense of Alston and Turner (1963) and the individuals with complementary chromatographic profiles, therefore, are probably F_1 hybrids. The three putative hybrids (*Windler* 4081-12, 20 and 21) that do not exhibit complementation are the same ones that were noted earlier as being somewhat separated from the other putative hybrids (Fig. 1, arrows). Their flavonoid profiles are similar to *M. ringens* and they may, as suggested earlier, represent backcross individuals. Levin (1967, 1968), for example, found that backcross individuals of *Phlox* and *Liatris* usually have the chromatographic profile of the recurrent parent and contain none of the compounds of the non-recurrent parent. That the above three plants are indeed backcrosses and not variable *M. ringens* individuals is further substantiated by other data that show that they are fairly well separated from the *M. ringens* plants morphologically, and more importantly they exhibit low percentages of pollen stainability when compared to the *M. ringens* individuals (see pollen stainability results).

SUMMARY

Morphological and chemical evidence as well as pollen stainability data indicate that extensive hybridization is occurring in the Patapsco River population. Furthermore, morphological and chemical data are in agreement that at least limited backcrossing to *Mimulus ringens* is taking place. However, pollen data strongly suggest that backcrossing has not been extensive and, therefore, the morphological variability in *M. ringens* noted in the scatter diagram is probably due to phenotypic plasticity and is not the result of introgression.

LITERATURE CITED

ALSTON, R. E., & B. L. TURNER. 1963. Natural hybridization among four species of *Baptisia* (Leguminosae). Amer. J. Bot. **50**:159-173.

LEVIN, D. A. 1967. Hybridization between annual species of *Phlox:* population structure. Amer. J. Bot. **54**: 1122-1130.

————. 1968. The structure of a polyspecies hybrid swarm in *Liatris*. Evolution **22**: 352-372.

MABRY, T. J., K. MARKHAM, & M. THOMAS. 1970. The systematic identification of flavonoids. Berlin: Springer-Verlag.

PENNELL, F. W. 1935. The Scrophulariaceae of eastern temperate North America. Philadelphia Acad. Sci. Monogr. **1**: 123-136.

STEEL, R. G. D., & J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill, Inc. New York. 481p.

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THE TAXONOMY OF POTAMOGETON SUBSECTION HYBRIDI IN NORTH AMERICA

A. A. Reznicek and R. S. W. Bobbette

Potamogeton subsection *Hybridi* is a very distinctive group of small, linear-leaved Pondweeds. Especially characteristic of the group are stipules adnate to the leaf base with the free tip projecting as a ligule, the ability to fruit freely with or without floating leaves, and fruits with a conspicuous cochleate embryo. The unusual, flattened fruits distended by the easily visible spiral of the embryo are unique to this subsection.

The group is restricted to the Americas where it is widely distributed from Newfoundland south to Cuba and central Mexico and west to California and southern British Columbia. One representative is found in Brazil (Fernald, 1932, 1950; Hitchcock and Cronquist, 1973).

The general ecology of the North American species is similar in many respects. It is here briefly described as some ecological features are of importance taxonomically. The species usually occur in rather shallow water, growing near shores, in streams and in shallow ponds and bays. They are sometimes found in only a few inches of water. All will grow more or less exposed on mudflats and shores producing a terrestrial form with much shortened internodes and only dilated leaves. Observations in the field and examination of specimens indicate that all the species may be either annual or perennial in duration. They may perennate by persistent bases and rhizomes or by poorly differentiated winter buds.

From a taxonomic standpoint, the group has long been a source of considerable confusion. The number of species

recognized in North America in contemporary works varies from two, *Potamogeton spirillus* Tuckerman and *P. diversifolius* Rafinesque (Ascherson and Graebner, 1907; Taylor, 1909; Gleason, 1952), to four: *P. spirillus, P. diversifolius, P. capillaceus* Poiret and *P. bicupulatus* Fernald (Fernald, 1932, 1950). The difference in opinion as to the number of species is a result of the separation of *P. diversifolius* sensu lato into three species by Fernald (1932). Our investigation was prompted by the collection of a fine-leaved *Potamogeton* belonging to subsection *Hybridi* which was not previously known to occur in Canada. Initial attempts to name the specimens and related material proved unsatisfactory and further research was undertaken.

MATERIALS AND METHODS

This study is based on approximately 1850 specimens borrowed from the following herbaria: ACAD, CAN, DAO, ILL, GH, MIN, MO, NCU, TRT, NY, QK, TEX, UARK, US, USF, UWM, and the herbarium of the Algonquin Park Museum. In addition, populations of *Potamogeton spirillus* and *P. bicupulatus* were examined in the field in Canada.

THE SEPARATION OF POTAMOGETON SPIRILLUS

Potamogeton spirillus is regarded as distinct by all contemporary authors. Our observations have shown it to be easily distinguished from the other two taxa[1] of this group by a number of features. These features are summarized in Table 1. Figs. 1 and 2 illustrate the differences in the fruits and the degree of stipule fusion.

[1]As will be shown subsequently, there are two other taxa in this subsection; a fine leaved northern plant called *Potamogeton bicupulatus* and a broader leaved, more southern species called *P. diversifolius*. They are referred to by these names in these and following figures.

Table 1: Distinction of *P. spirillus*

P. spirillus	*P. bicupulatus and P. diversifolius*
Fruits without lateral keels	Fruits usually with lateral keels
Fruits 1.3-2.4 mm in diameter	Fruits 0.9-2.0 mm in diameter
Peduncle of submersed spike up to 3 mm	Peduncle of submersed spikes 1-10 mm
Fused portion of stipules longer than free ligule	Fused portion of stipule shorter than free ligule
Phyllodal leaves 15-80 times longer than wide	Phyllodal leaves 20-500 times longer than wide
Phyllodal leaf tips usually rounded to subacute	Phyllodal leaf tips obtuse to setaceous

THE POTAMOGETON DIVERSIFOLIUS COMPLEX

Prior to Fernald's (1932) excellent work, two species were recognized in the subsection by monographers (Morong, 1893; Ascherson and Graebner, 1907; Taylor, 1909): (1) *Potamogeton spirillus,* incorrectly called by these authors *P. dimorphus,* and (2) *P. diversifolius,* incorrectly called *P. hybridus* by Ascherson and Graebner. The distinctions they used to separate the two were in the main those given here for separating *P. spirillus* from the other taxa.

Fernald (1932) greatly clarified the nomenclature and expanded the taxonomy of the subsection. He recognized three taxa other than *Potamogeton spirillus: P. diversifolius, P. capillaceus* and *P. bicupulatus.* These latter three species can be regarded as the *P. diversifolius* complex. *Potamogeton diversifolius* was treated as a wide ranging species with phyllodal leaves acute to obtuse and 0.5 to 2 mm wide, rounded dilated leaves and short peduncled submersed spikes. *Potamogeton bicupulatus* and *P. capillaceus* he recognized as similar to each other vegetatively,

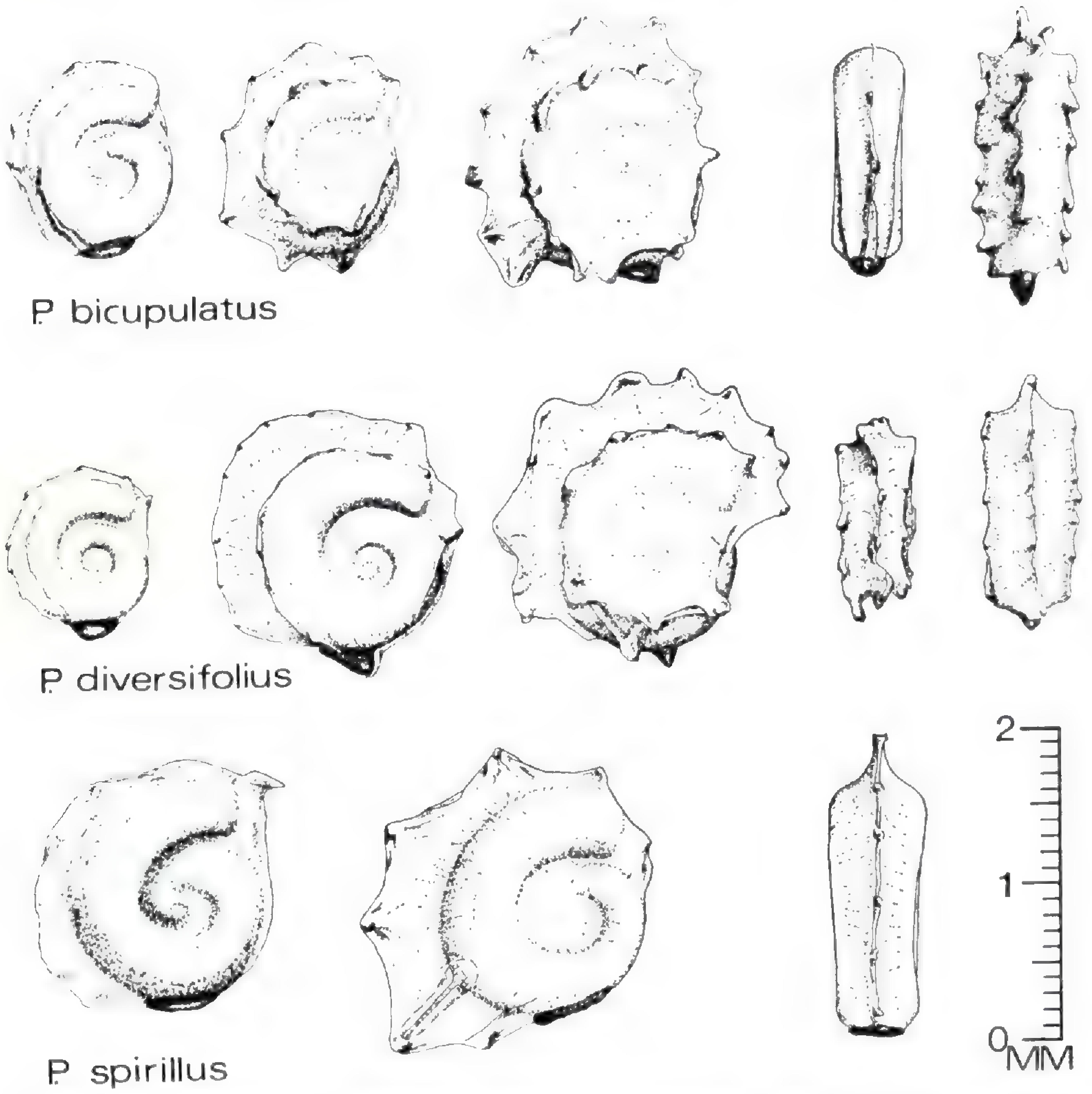

Fig. 1. Fruits of *Potamogeton bicupulatus* (top), *P. diversifolius* (middle), and *P. spirillus* (bottom).

and both differing from *P. diversifolius* in having phyllodal leaves setaceous, 0.1 to 0.6 mm wide, acute dilated leaves and longer peduncled submersed spikes. Fernald differentiated between the two on the basis of the fruits. *Potamogeton capillaceus* he considered a coastal species with flat sided olive fruits 1 to 1.5 mm wide and the former a rare plant of the Allegheny Mountains with 1.6 to 2.2 mm wide fruits that were stramineous with crateriform sides.

Klekowski and Beal (1965) investigated *Potamogeton capillaceus* and *P. diversifolius* in the Carolinas. They showed complete intergradation of the characters used to separate the two and presented strong evidence that it was

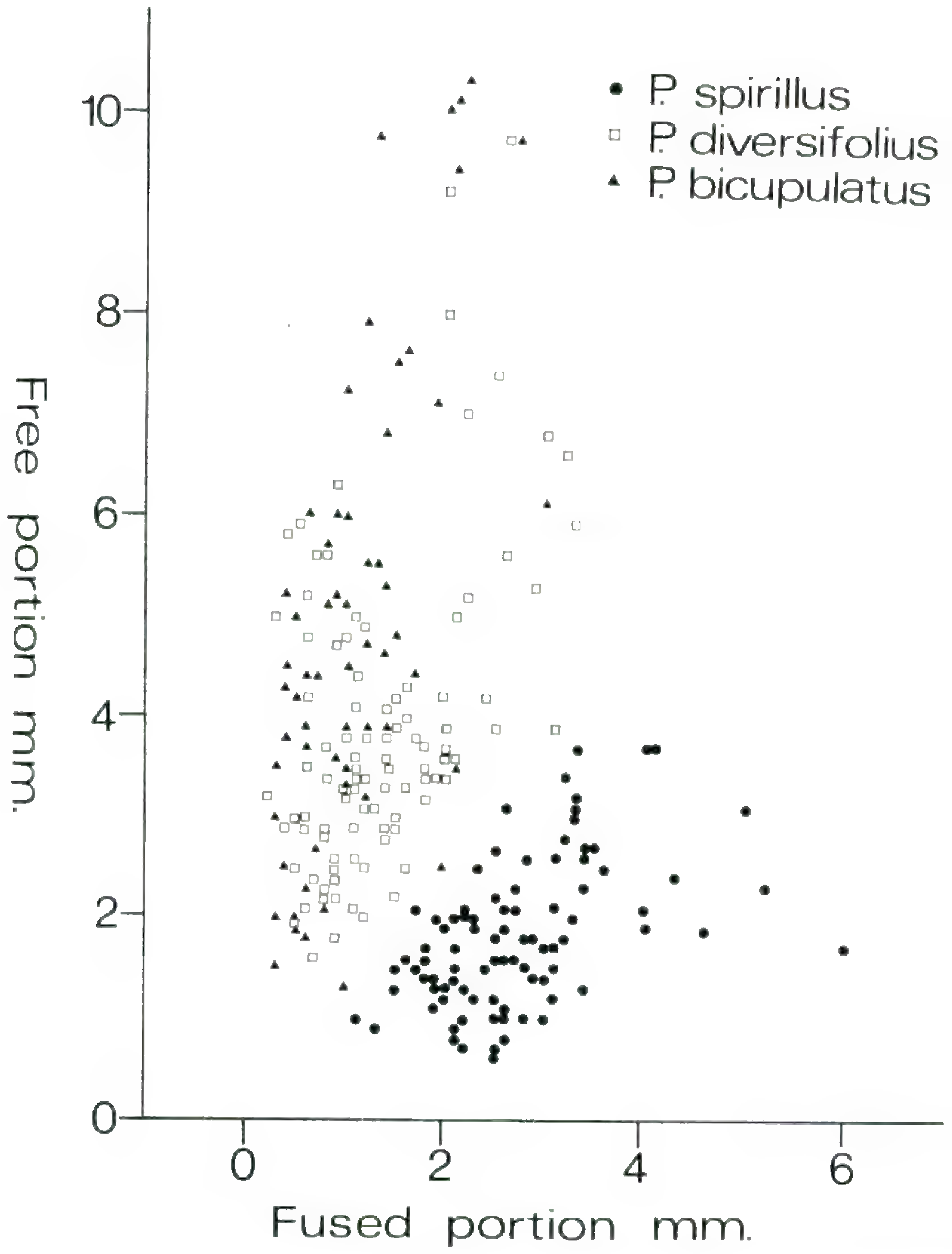

Fig. 2. Scatter diagram of length of free portion of stipule against length of portion fused with the leaf for *Potamogeton spirillus*, *P. diversifolius* and *P. bicupulatus*.

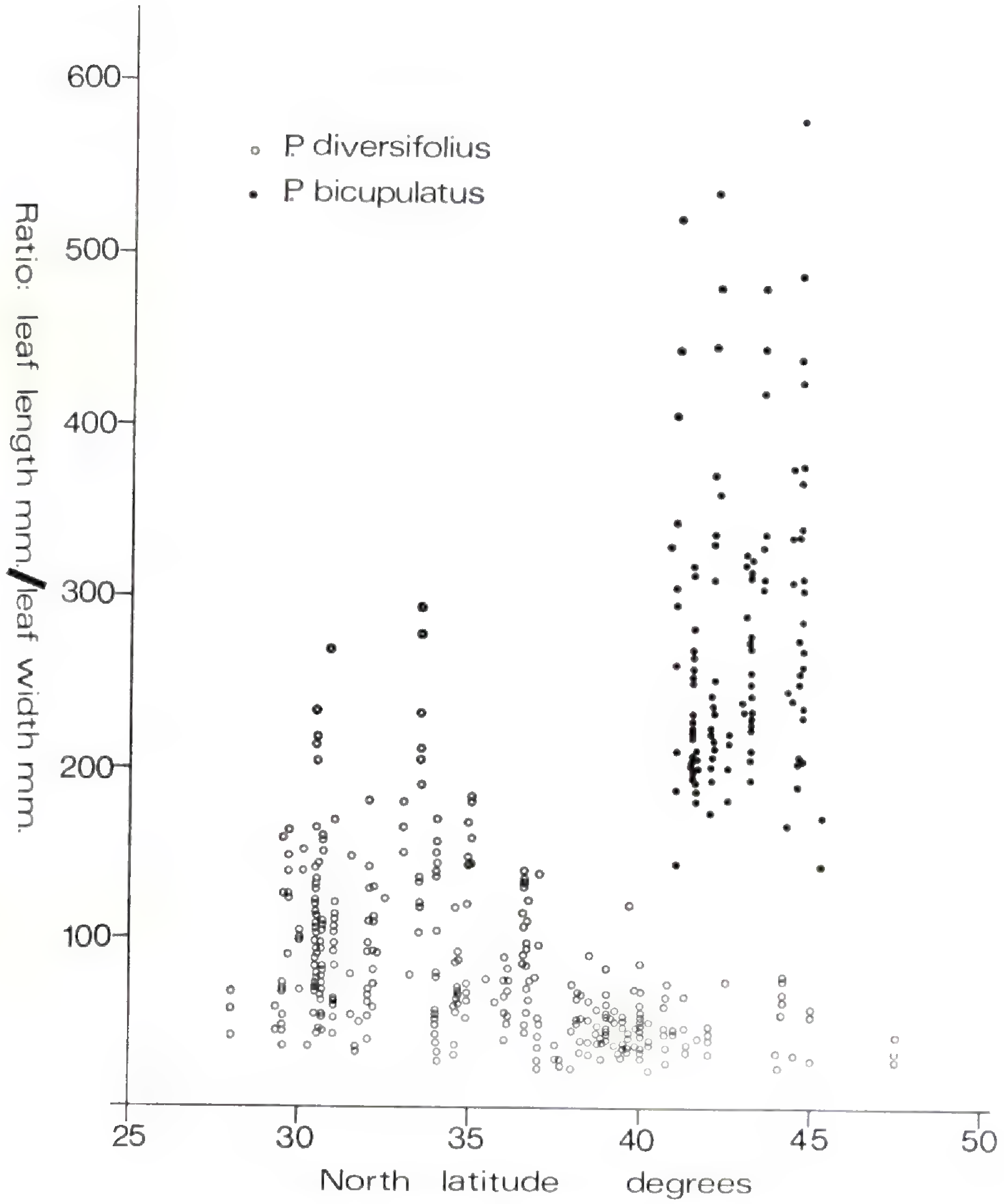

Fig. 3. Scatter diagram of phyllodal leaf length:width ratio against north latitude for *Potamogeton diversifolius* and *P. bicupulatus.*

not possible to recognize two taxa in the Carolinas. In spite of this evidence, Voss (1972b) felt that Michigan plants referable to *P. capillaceus* appeared distinct from *P. diversifolius*. These authors did not deal with *P. bicupulatus.*

When specimens of this complex were examined over their entire range, several most notable trends came to light. After a preliminary examination of many features, it was found that phyllodal leaf characters showed distinct discontinuities. These discontinuities were in leaf width, the leaf length-width ratio and the widest leaf present.

Figure 3 is a scatter diagram of leaf length:width ratios versus the latitude of the collection locality. Two clearly separate groups are illustrated. One is a very fine leaved northern taxon with leaf length:width ratios of about 200 to 600 that occurs from latitude 40 to 45 degrees north; the other a variable taxon that is wide ranging from latitude 25 to 48 (but generally more southern) and has a leaf length:width ratio of 30 to rarely more than 200. The two groups shown in Fig. 3 again separate clearly when the width of the widest phyllodal leaf is used in place of latitude (Fig. 4). Also, Fig. 5 shows a frequency diagram of leaf width. Again, two groups show as distinct entities. Other features such as dilated leaf length:width ratios and emersed spike length followed the same pattern but showed more overlap. We do not hesitate to recognize the two groups as different taxa at the specific level.

Fernald's annotations, and comparison of specimens with his descriptions, clearly indicate that the fine leaved northern plant was the major basis for his concept of *Potamogeton capillaceus*. The broader leaved southern plants are *P. diversifolius.*

Also clear from Fig. 3 is that wherever the two taxa occur at the same latitude, they do not approach each other in phyllodal leaf length:width ratio. Only where *Potamogeton diversifolius* occurs well south of the range of the northern fine leaved taxon do the values for this ratio approach each other. This is a very interesting displace-

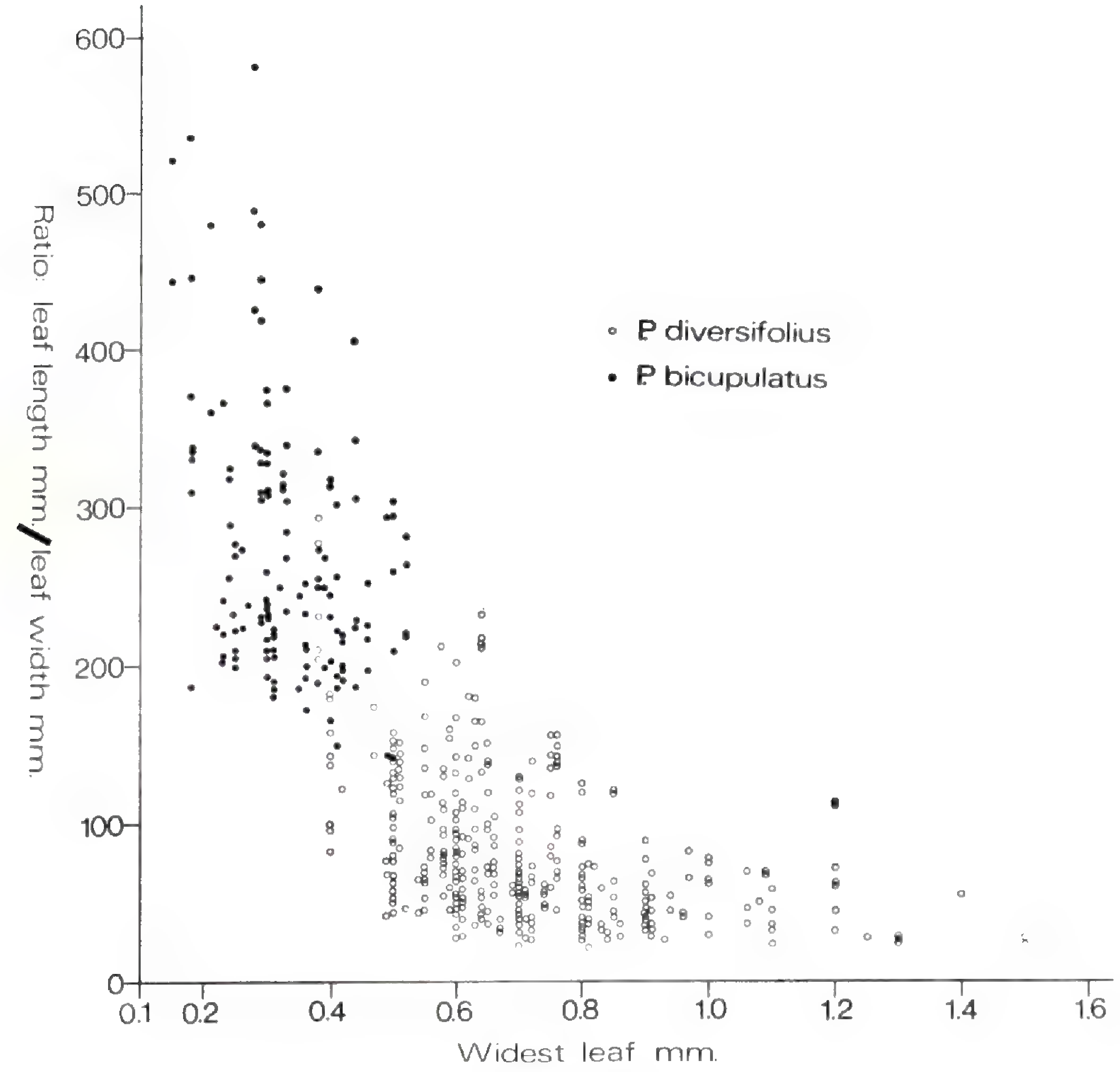

Fig. 4. Scatter diagram of phyllodal leaf length:width ratio against the widest phyllodal leaf for *Potamogeton diversifolius* and *P. bicupulatus*.

ment of characters. Fernald also considered *P. capillaceus* to include the finest leaved extreme of the southern plants. However, as Klekowski and Beal (1965) showed, they are indistinguishable from and merge completely with *P. diversifolius*. The only discontinuity shown in Fig. 3 occurs well north of the Carolinas.

That the southern plants are not merely more robust forms of the northern is clear. Figure 3 shows that there is a discontinuity of several degrees of latitude where there are no very fine plants. Secondly, there are rarely any actual overlaps in the measurements. Two specimens from

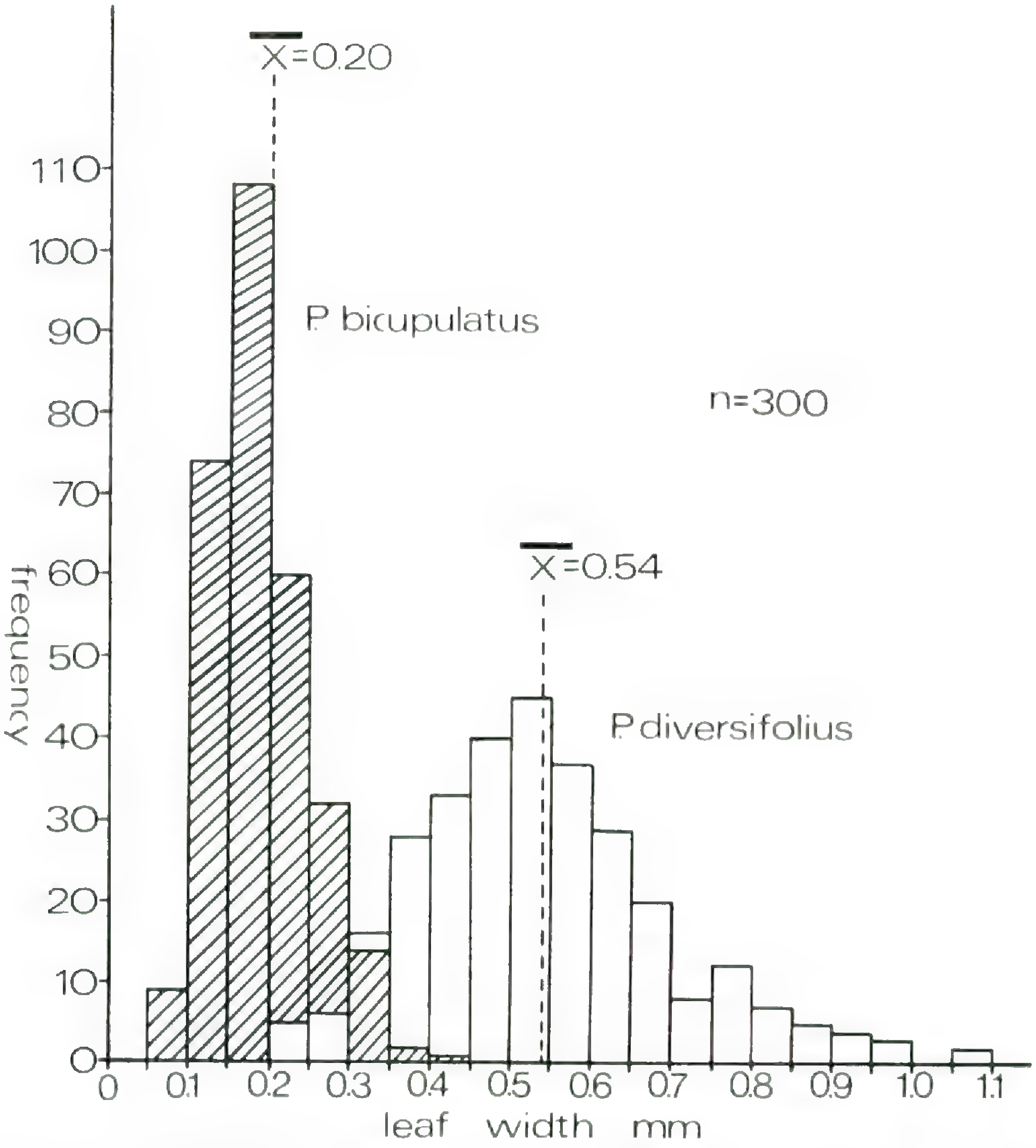

Fig. 5. Frequency histogram of phyllodal leaf width for 300 measurements each of *Potamogeton bicupulatus* and *P. diversifolius.*

the south were seen, both from lime sinks, that did overlap (*Radford* 7924, Florida, DAO; *Massey* et al. 2941, South Carolina, NCU). These two puzzling specimens are mostly responsible for what overlap there is in the graphs and are here considered rare extremes of *Potamogeton diversifolius.* Also, although there are considerable differences in the phyllodal leaves, the northern and southern taxa have fruits that are virtually identical in size. However, when finer leaved southern plants (widest leaf less than 0.6 mm) were measured, their fruits were distinctly smaller

(Table 2). This observation would not be expected if the southern fine leaved plants that Fernald (1932) considered *P. capillaceus* were more robust individuals of the northern fine leaved taxon. It indicates that the finer leaved southern plants are simply small extremes of *P. diversifolius.*

Table 2: Fruit diameters of *P. diversifolius* complex.

Species	Sample Size	Mean (mm)
P. bicupulatus	450	1.43
P. diversifolius		
Fine-leaved	128	1.36
Broad-leaved	322	1.42

THE IDENTITY OF POTAMOGETON BICUPULATUS FERNALD

Potamogeton bicupulatus was distinguished from *P. capillaceus* mainly by fruit size, color and sculpturing (Fernald, 1932). However, examination of specimens has not borne out the differences in color, and the sculpturing, based on the degree of development of the keels, was found to be extremely variable. No discontinuities were found in either feature. Figure 6 shows two frequency diagrams for fruit size for the northern fine leaved taxon and *P. diversifolius.* With a large sample it is easy to see that the fruits of the two species can range to extremes up to 2 mm. This is near the maximum size of 2.2 mm given for *P. bicupulatus* and well above the maximum of 1.5 mm stated by Fernald (1932) for *P. diversifolius* and *P. capillaceus.* Plants considered by Fernald as *P. bicupulatus* are extremes of fruit size and sculpturing.

The situation proved more complex when examined in detail. Fernald (1932) recorded three localities for his species: Vermont, Pennsylvania and Tennessee. The Vermont report was based on a single specimen (*Chapman,* s.n. Lake Dunsmore, Vt. (MO!). The specimen was doubted by Fernald and is clearly an error. The plant is *Potamogeton diversifolius* and unquestionably the locality is incor-

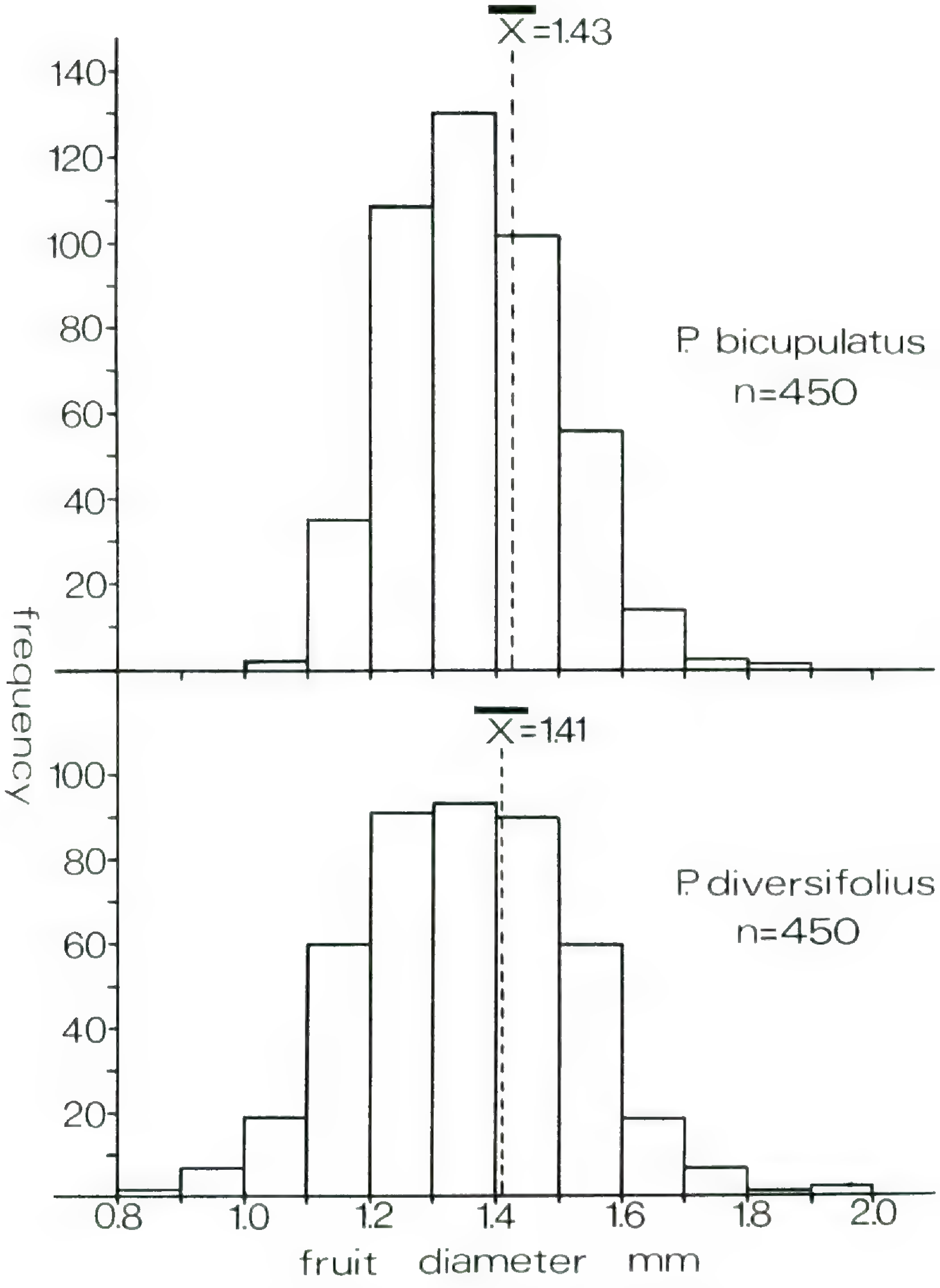

Fig. 6. Frequency histogram of fruit diameter for 450 measurements each of *Potamogeton bicupulatus* and *P. diversifolius.*

rect. When specimens from the other two areas were examined, it was found that the plants from Pennsylvania were exceedingly fine leaved with length:width ratios over 200 and the plants from Tennessee were wider leaved with length:width ratios well under 200. Figure 7 shows a frequency diagram of leaf width for plants from the two areas. When this is compared with Fig. 5 one can see that the Pennsylvania plants are clearly the northern fine leaved taxon and the Tennessee specimens are *P. diversifolius*. *Potamogeton bicupulatus*, as conceived by Fernald, consisted of localized populations of large fruited extremes of these two similar species. The name, however, applies to the northern fine leaved taxon as the type is from Pennsylvania.

NOMENCLATURE

Our investigations have confirmed Fernald's (1932) application of the names *Potamogeton spirillus* Tuckerman and *P. diversifolius* Rafinesque. The question of the correct name for the northern fine leaved taxon, however, must be settled. As discussed before, Fernald's concept of *P. capillaceus* was based mainly on this northern taxon. However, the type of *P. capillaceus* was stated to be from 'Caroline septentrionale' (Poiret, 1816). Voss (1972a) searched for this type and indicated that it might be in Herb. Desfontaines at Florence. Following his suggestion, this proved to be the case and when a photograph was obtained, the specimen was *P. diversifolius* with phyllodal leaves up to 0.8 mm wide. The name *P. capillaceus* must be relegated to synonymy under *P. diversifolius*.

A scrutiny of all available names revealed that the earliest name that applies to the northern fine leaved taxon is *Potamogeton diversifolius* var. *trichophyllus* Morong (type from New Jersey); however, the earliest name for the taxon applied at the specific level is *P. bicupulatus* Fernald (type from Pennsylvania). Fernald (1932) presented evidence that *P. dimorphus* Rafinesque (1817), based on *P.*

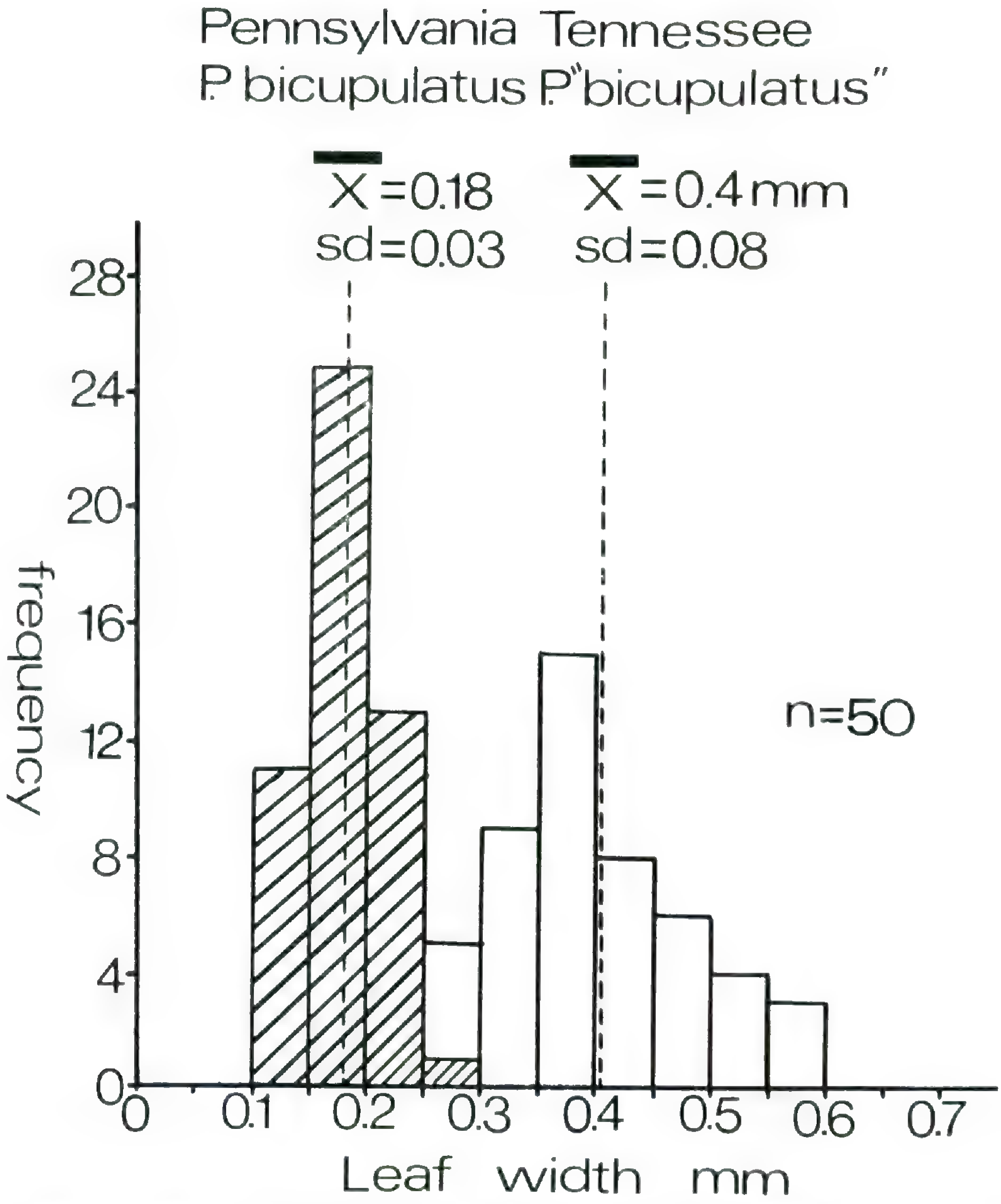

Fig. 7. Frequency histogram of phyllodal leaf width for 50 measurements each of Pennsylvania *Potamogeton bicupulatus* and Tennessee *P. "bicupulatus"*.

diversifolious W.P.C. Barton, also applies to the northern fine leaved taxon. However, he contrasts Barton's plant only with *P. spirillus* and does not mention the possibility of the plant being *P. diversifolius* Rafinesque nor for that matter his own *P. bicupulatus.* When the herbarium of W.P.C. Barton was consulted, there was no type. Pennell (1942) discusses the fact that the larger part of Barton's herbarium is lost. As all three species of this subsection occur in the Philadelphia region, there is no possibility of being completely certain of the application of the name with only the description given by Barton (1815). Without a type, the identity of *P. dimorphus* Rafinesque must be considered in doubt. We here use the oldest name at specific level whose application to the northern fine taxon is certain, *P. bicupulatus* Fernald. If the type of *P. dimorphus* Rafinesque should be found, that name may prove to apply here.

PRACTICAL TAXONOMIC DIFFICULTIES

Before the taxonomic treatment is introduced, it must be noted that some taxonomic difficulties encountered with these Potamogetons stem from problems in accurately observing the extremely fine parts of the plant. The widths of the phyllodal leaves ranged mostly from 0.1 to 1.0 mm and the lengths from 3 to 11 cm. On most collections, the very long, narrow leaves of the finest species were usually broken and almost invariably bent and folded. Accurate measurement of the dimensions required measuring to 0.01 mm for phyllodal leaf width and the use of extreme care to make sure that the full length of the leaf was intact. It was not possible to measure all specimens. Many poorer collections showed no complete leaves. The importance of good herbarium specimens in this group cannot be overemphasized.

Our experience indicates that the best technique for making specimens of these Potamogetons is to float the plants onto a more or less stiff sheet of well sized heavy

bond paper somewhat smaller than the herbarium sheet. After pressing and drying in the usual manner between newsprint, the sheet should be placed inside a large packet on the herbarium sheet. No glue need be applied to the plant.

When measuring specimens for identification, care must be taken to avoid leaves that are beginning to show a transition to dilated leaves. This transition is very gradual and easily overlooked. The first leaves of the year at the base of the plant, leaves that are from late fall shoots and proliferating shoots from the axils of floating leaves should also be avoided. The leaves to measure are mature leaves on the middle parts of main stems. Seedling plants of this group also may cause difficulties as they will be small in most measurements although they may bear fruit. Terrestrial forms and collections with only dilated leaves are often nearly impossible to determine. Flowing water forms also differ greatly in aspect but may usually be keyed out successfully. They do tend to have narrower leaves than usual.

KEY TO SPECIES[2]

1. Adnate portion of stipule mostly longer than free ligule, fruits with a dorsal keel and smoothly rounded sides. . . . . 1. ***P. spirillus***
1. Adnate portion of stipule mostly shorter than free ligule, fruits usually with two lateral, entire to toothed ridges forming a 'shoulder' or row of teeth on either side of the dorsal keel.
    2. Middle stem leaves 190 to 500 times as long as wide, usually 0.1 to 0.35 mm wide, averaging 0.2 mm. . . . . 2. ***P. bicupulatus***
    2. Middle stem leaves 20 to 180 times as long as wide, usually 0.3 to 1.5 mm wide, averaging 0.54 mm. . . . . 3. ***P. diversifolius***

[2]The term leaf as used in the key refers to the phyllodal leaves.

TAXONOMIC TREATMENT[3]

1. *Potamogeton spirillus* Tuckerman, Amer. Jour. Sci. and Arts, Ser. 2, 6:228, 1848. Type locality: Charles and Mystic Rivers, Massachusetts. Type not traced.

Plant up to 10 dm, bushy at base, mostly with a few elongate stems, these sparsely branched; with or without dilated leaves. Dilated leaves 7-35 mm long, 2-13 mm wide, lanceolate-elliptic to elliptic-ovate, obtuse, tapering to rounded at base with 5-13 veins strongly impressed beneath; petiole 5-25 mm. Stipules of dilated leaves 3-15 mm, membranaceous to ± fibrous, free from leaf base. Phyllodal leaves 8-80 mm long, 0.5-2 mm wide, linear, flat, 15-80 times as long as wide, rounded to acute, 1-3 veined, usually with a lacunar band bordering midvein. Stipules 2-12 mm, membranaceous, fused with the leaf for 1.5-6 mm, fused for half or more of the total length. Fruiting spikes dimorphic, spikes in the axils of phyllodal leaves 2-5 mm in diameter, 1-8 fruited, globular; peduncle up to 3 mm, recurved. Transitional to spikes in the axils of dilated leaves; these 4-13 mm long, 4-5 mm wide, 4-35 fruited, ellipsoid to cylindric; peduncles 4-27 mm, slightly clavate. Fruits 1.3-2.4 mm in diameter, ± orbicular, olive-green to stramineous, flattened, keeled. Dorsal keel entire to sinuate, lateral keels absent. Beak minute. Fruit concave sided, distended by the cochleate embryo.

The distribution of this common northern species is mapped in Fig. 8. Tuckerman's excellent description of the plant is very clear and he carefully contrasted his plant with *Potamogeton bicupulatus* (sub *P. hybridus* Michaux), the only other related species occurring in Massachusetts. There is no doubt that his name applies to this distinctive little pondweed.

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[3]Synonymy is cited only where it differs from that given in Fernald (1932).

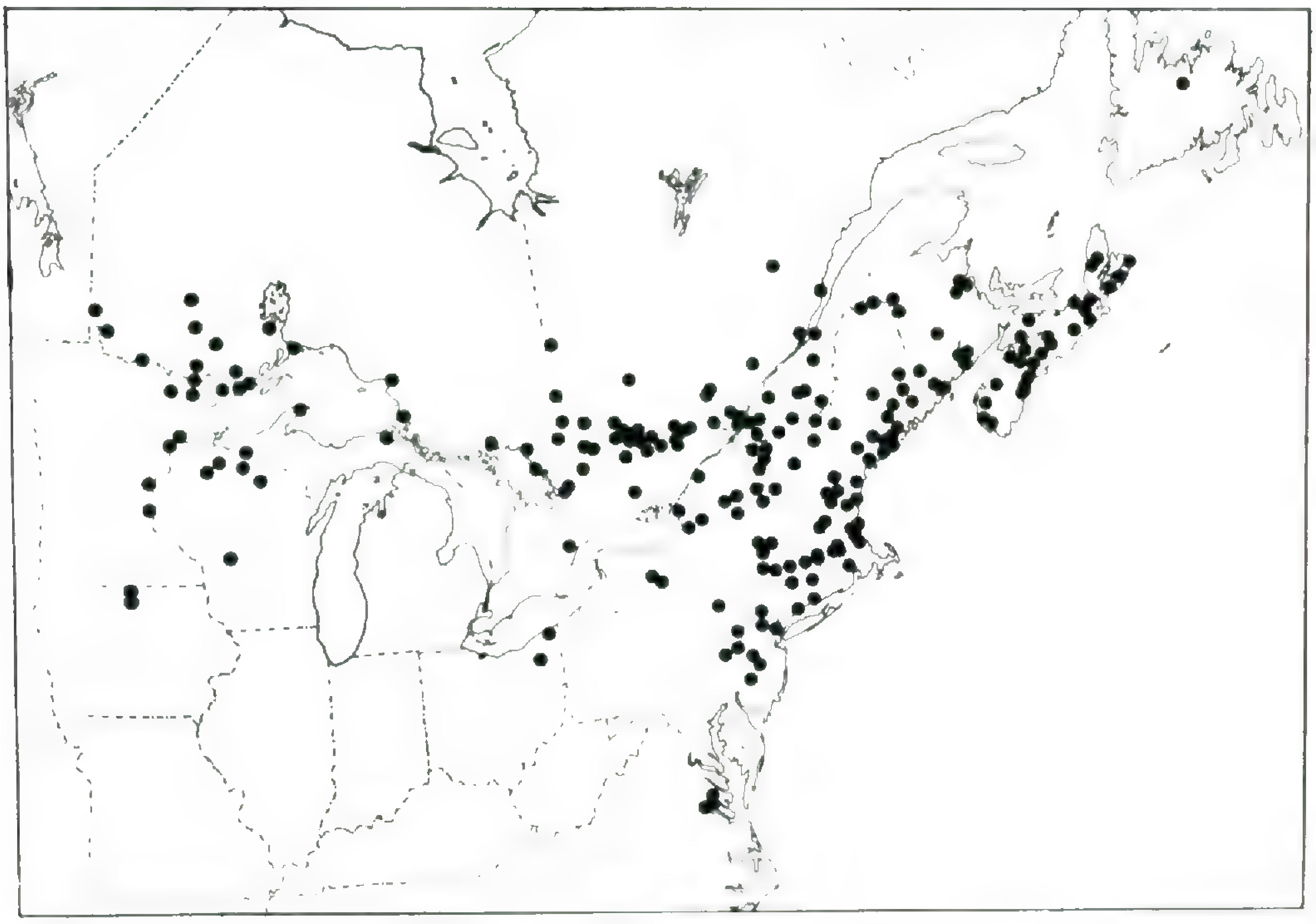

Fig. 8. Distribution of *Potamogeton spirillus*.

2. *Potamogeton bicupulatus* Fernald, Mem. Am. Acad. 17: 112, 1932. Holotype: Lehigh Co., Pennsylvania, *A. P. Garber* 1866 PH, photo TRTE (!). Probable isotypes: GH (!), QK (!). (These specimens bear the additional data: Lehigh water gap, Blue Mts.)

P. diversifolius Raf. var. *trichophyllus* Morong, Mem. Torr. Bot. Club. 3: 49, 1893. Holotype: Lake Marcia, Sussex Co., New Jersey, *N.L. Britton*, Aug 31, 1883. NY (!).

Plant up to 11 dm, bushy at base, mostly with a few elongate stems, these sparsely branched; with or without dilated leaves. Dilated leaves 6-23 (28) mm long, 2-11 mm wide, lanceolate-elliptic to broadly elliptic, acute, tapering to rounded at base with 3-7 veins strongly impressed beneath; petiole 5-35 mm. Stipules of dilated leaves 3-11 mm, membranaceous, free from leaf base. Phyllodal leaves 30-110 mm long, 0.08-0.4 (0.5) mm wide, setaceous, 190-500

(600) times as long as wide, long acuminate to setaceous, 1 veined. First leaves of the season, leaves transitional to dilated leaves and leaves of shoots produced late in the fall may be shorter and wider, sometimes as little as 140 times as long as wide. Stipules 2-12 mm, membranaceous fused with the leaf for 0.3-3.5 mm, fused for less than half of the total length. Fruiting spikes dimorphic, spikes in the axils of phyllodal leaves 1.5-7 mm long, 1.5-5 mm wide, 1-15 fruited, globular to ellipsoid, peduncle 1-10 mm, ± recurved, clavate. Transitional to spikes in the axils of dilated leaves; these 3-14 mm long, 2.5-4.5 mm wide, 5-40 fruited, ellipsoid to cylindric; peduncle 3.5-22 mm, slightly clavate. Fruits 1.1-2.0 mm in diameter, ± orbicular, olive-green to stramineous, flattened, keeled, dorsal keel entire to dentate, two lateral keels usually present, often consisting of isolated teeth, sometimes entire. Beak minute. Fruit concave sided, usually distended by the cochleate embryo.

This very delicate pondweed is illustrated in Fig. 9a and its distribution mapped in Fig. 10. Although mainly eastern, it has outlying stations near Georgian Bay, Ontario, at the head of Lake Michigan in Michigan and Indiana and in central Wisconsin and Minnesota. This is a distribution pattern shown by many more coastal species (Peattie, 1922; McLaughlin, 1932). In Ontario, *Potamogeton bicupulatus* occurs in the shallow soft water of Canadian Shield Lakes with peaty or sandy bottoms. These lakes are notable for the large number of rare and unusual aquatic plants that they possess. As well as *P. bicupulatus*, included are: *Isoetes macrospora, Potamogeton oaksianus, Eleocharis robbinsii, Juncus militaris, J. pelocarpus, Eriocaulon septangulare, Elatine minima, Myriophyllum tenellum, M. farwellii, Nymphoides cordata, Gratiola aurea, Utricularia resupinata, U. purpurea* and *Littorella americana.*

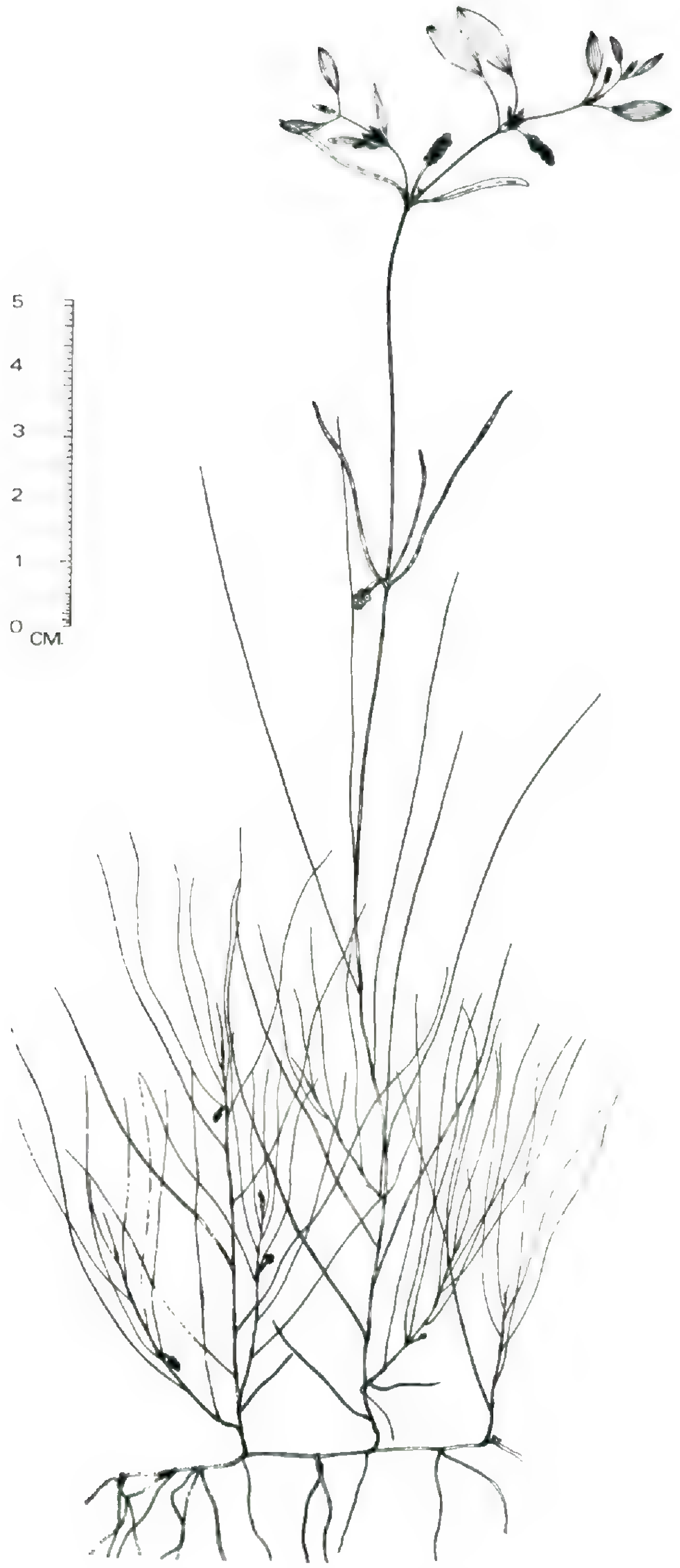

Fig. 9a. Habit of *Potamogeton bicupulatus*.

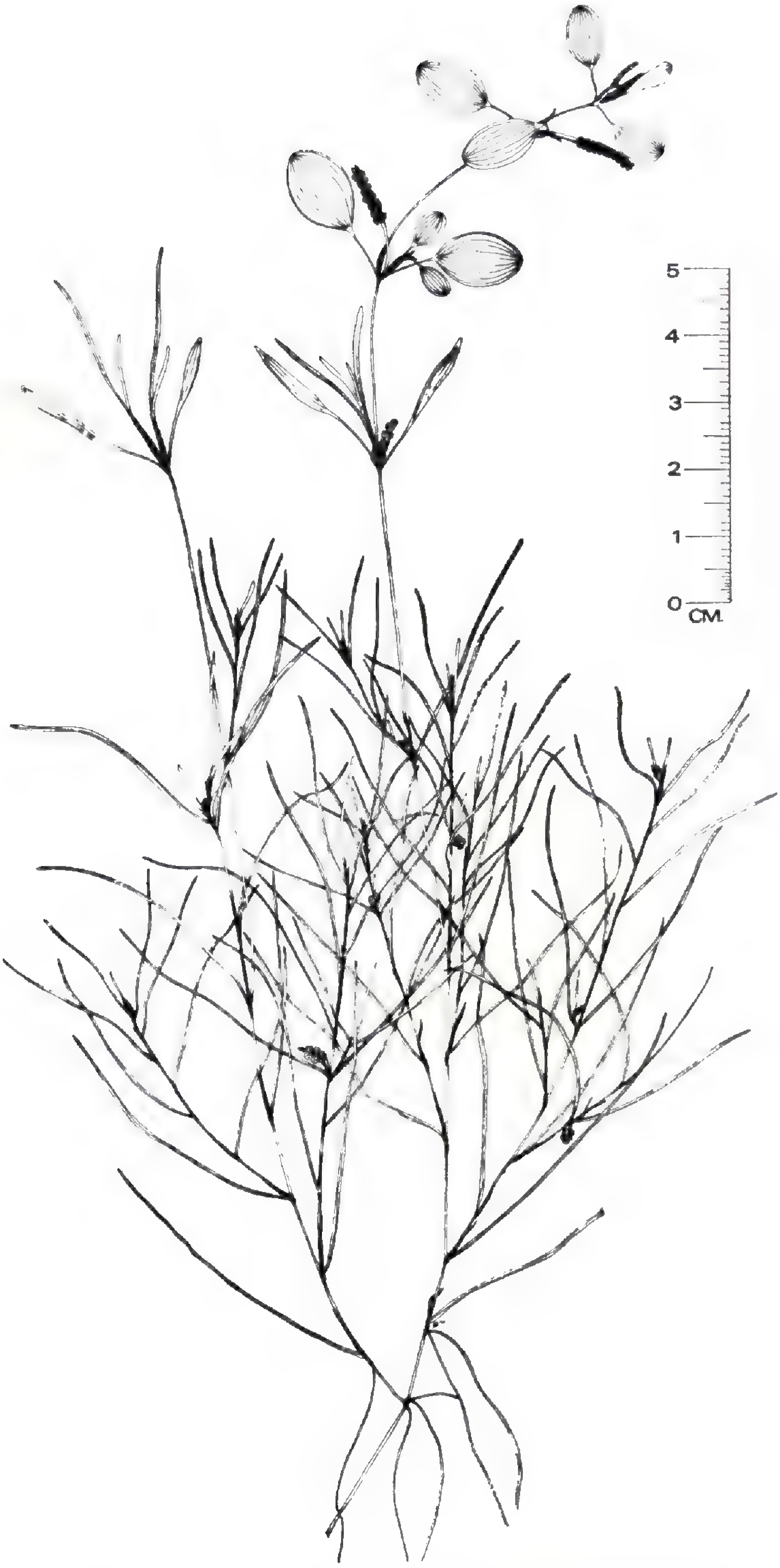

Fig. 9b. Habit of *Potamogeton diversifolius.*

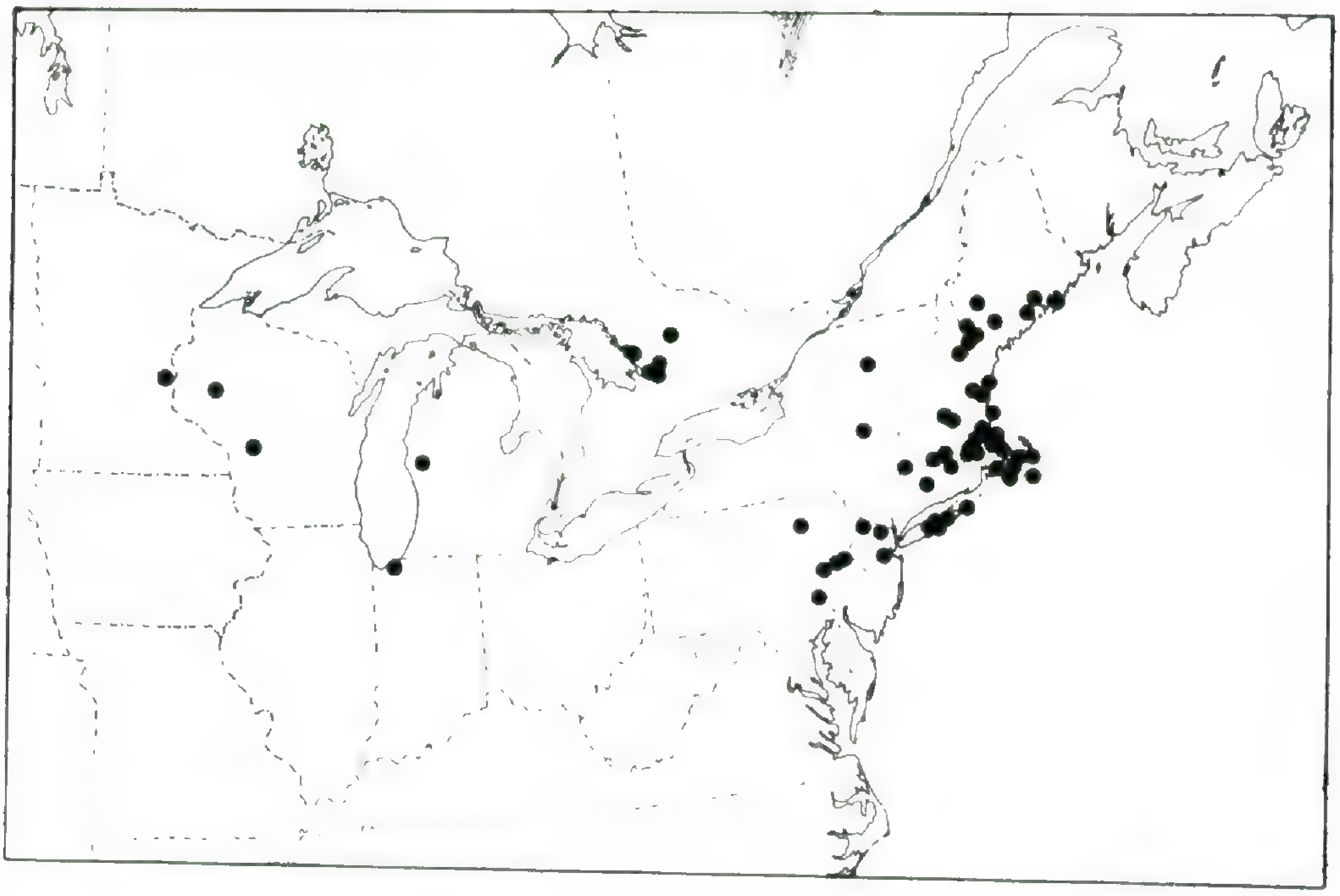

Fig. 10. Distribution of *Potamogeton bicupulatus.*

3. *Potamogeton diversifolius* Rafinesque, Med. Repos. 2. 5: 354, 1808. Based on *P. hybridus:* var. β Michaux, Fl. Bor. Am. 1: 101, 1803. Holotype in Herb. Michaux: In stagnis Carolina, *Michaux.* P n.v.

P. capillaceus Poiret, Encyc. Meth. Bot. Suppl. 4: 535, 1816. Holotype in Herb. Desfontaines: Caroline septentrionale, *M. Delisle.* FI, photo TRTE (!). (Original label missing from specimen.)

P. diversifolius var. *multidenticulatus* Morong, Mem. Torr. Bot. Club 3: 48, 1893. Holotype: Rehoboth City, Delaware, *G. F. Parker,* Aug. 17, 1878. NY (!).

P. capillaceus var. *atripes* Fernald, Rhodora 39: 380, 1937. Holotype: Jones Hole Swamp, Coddyshore, Sussex Co., Virginia, *Fernald & Long* 5976, July 20, 1936. GH (!). Isotypes: NY (!), US (!), MO (!).

Plant up to 15 dm, ± bushy at base, mostly with elongate, ± branched stems; with or without dilated leaves. Dilated leaves 5-40 mm long, 2-20 mm wide, lanceolate-elliptic to ovate or obovate to suborbicular, acute to rounded, tapering to rounded at base with 3-17 veins

strongly impressed beneath; petiole 2-40 mm. Stipules of dilated leaves 2-25 mm, membranaceous to ± fibrous, free from leaf base. Phyllodal leaves, 10-80 (110) mm long, (0.25) 0.35-1.5 mm wide, linear, flat, 20-150 (280) times as long as wide, obtuse to long acuminate, 1 (3) veined, larger leaves with a lacunar band. Stipules 2-18 mm, membranaceous, fused with the leaf for 0.3-4.0 mm, fused for less than half of the total length. Fruiting spikes dimorphic, spikes in the axils of phyllodal leaves 1.5-6 mm long, 1.5-5 mm wide, 1-15 fruited, globular to ellipsoid; peduncle 1-8 mm, ± recurved, slightly clavate. Transitional to spikes in the axils of dilated leaves; these 3-28 mm long, 2.5-5 mm wide, 5-120 fruited, ellipsoid to cylindric; peduncle 3-32 mm, slightly clavate. Fruits 0.9-2.0 (2.2) mm in diameter, ± orbicular, olive-green to stramineous, flattened, keeled, dorsal keel entire to dentate, two lateral keels usually present, entire to dentate. Beak minute. Fruit flat sided to concave, often distended by the cochleate embryo.

This wide ranging *Potamogeton* is illustrated in Fig. 9b and its distribution mapped in Fig. 11. Fernald's (1937) *P. capillaceus* var. *atripes* is here not considered worthy of separation, the black, rigid rhizomes being certainly a result of the plants' anomalous habitat.

We have also found, as did Klekowski and Beal (1965), that the narrowest leaved plants of *Potamogeton diversifolius* tend to occur on the coastal plain. This trend is especially evident, judging from herbarium records, on the gulf coastal plain. However, as Klekowski and Beal (1965) showed, they merge completely with broader leaved *P. diversifolius* and are here not viewed as a separate taxon.

ACKNOWLEDGMENTS

The authors wish to thank the Curators of all the Herbaria for the loans upon which this study is based, Dr. Carlo H. Steinberg of the Herbarium Universitatis Florentinae (FI) who kindly sent a photograph of the type of

Potamogeton capillaceus Poiret, Mr. John W. Braxton of the Academy of Natural Sciences of Philadelphia (PH) who sent a photocopy of the type of *P. bicupulatus* Fern. and searched for the type of *P. diversifolius* Barton, Dr. P. W. Ball who read the manuscript and provided critical comment, D. F. Brunton who informed us about Ontario records in Parry Sound and Nipissing Districts for *P. bicupulatus*, and R. E. Whiting who shared in discoveries of this species and *P. spirillus* in Muskoka District and Simcoe County, Ontario.

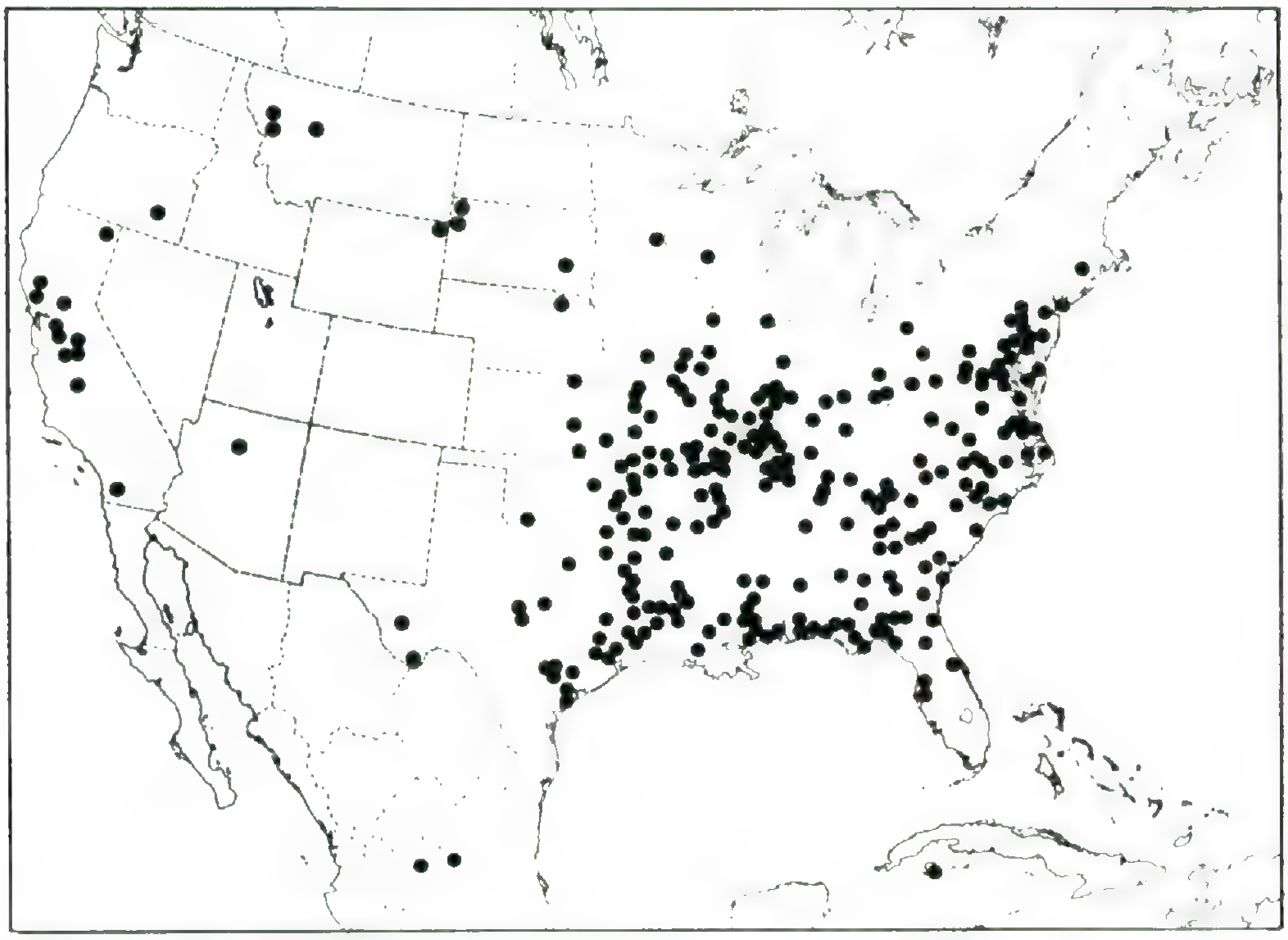

Fig. 11. Distribution of *Potamogeton diversifolius*.

LITERATURE CITED

ASCHERSON, P., & P. GRAEBNER. 1907. Potamogetonaceae. Das Pflanzenreich 4. 2: 1-184.

BARTON, W. P. C. 1815. Flora Philadelphica Prodromus. Philadelphia.

FERNALD, M. L. 1932. The linear-leaved North American Species of *Potamogeton*, Section Axillares. Mem. Am. Acad. 17: 1-183.

———. 1937. Local Plants of the Inner Coastal Plain of Southeastern Virginia. Rhodora **39**: 321-366, 379-415, 433-491.

———. 1950. Gray's Manual of Botany. Ed. 8. American Book Co., New York.

Gleason, H. A. 1952. The New Britton and Brown Illustrated Flora of the Northeastern States and Adjacent Canada. Hafner Publishing Co., New York. 3 vols.

Hitchcock, C. L. & A. Cronquist. 1973. Flora of the Pacific Northwest. An Illustrated Manual. University of Washington Press, Seattle. 5 vols.

Klekowski, E. J. & E. O. Beal. 1965. A Study of Variation in the *Potamogeton capillaceus-diversifolius* complex. Brittonia **17**: 175-181.

McLaughlin, W. T. 1932. Atlantic Coastal Plain Plants in the Sand Barrens of Northwestern Wisconsin. Ecol. Monogr. **2**: 335-383.

Morong, T. 1893. The Naiadaceae of North America. Mem. Torr. Bot. Club **3**: 1-65.

Peattie, D. C. 1922. The Atlantic Coastal Plain Element in the Flora of the Great Lakes. Rhodora **24**: 57-70, 80-88.

Pennell, F. W. 1942. Botanical Collectors of the Philadelphia Local Area. Bartonia **21**: 38-57.

Poiret, J. L. M. 1816. Encyclopédie Méthodique Botanique, Suppl. 4, Paris.

Rafinesque, C. S. 1817. Flora Philadelphica Prodromus, or Prodromus of the Flora Philadelphica, exhibiting a list of all the plants to be described in that work which have as yet been collected. By Dr. William P. C. Barton, Philadelphia, 1815. pp. 100. (review). Am. Monthly Mag. and Crit. Rev. **1**: 356-358. [1819].

Taylor, N. 1909. Zannichelliaceae. N. Am. Flora **17**: 13-27.

Voss, E. G. 1972a. Additional Nomenclatural and Other Notes on Michigan Monocots and Gymnosperms. Mich. Bot. **11**: 26-37.

———. 1972b. Michigan Flora, A Guide to the Identification and Occurrence of the Native and Naturalized Seed Plants of the State. Part I, Gymnosperms and Monocots. Cranbrook Institute of Science and University of Michigan Herbarium, Bloomfield Hills.

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MITRACARPUS (RUBIACEAE), A GENUS NEW TO FLORIDA AND EASTERN NORTH AMERICA

DANIEL B. WARD

The Rubiaceae has recently been seen as composed of twenty-nine tribes (Verdcourt, 1958), of which the *Spermacoceae* is represented in the southeastern United States by five genera: *Richardia, Diodia, Borreria, Spermacoce,* and *Ernodea.* To this assembly must now be added the genus *Mitracarpus,* represented by *M. villosus* (Sw.) DC., a species widespread in tropical America.

Members of the tribe *Spermacoceae* are separated by their modes of fruit dehiscence, which are remarkably diverse considering the presumed closeness of the associated genera. *Richardia* capsules split into three, and *Diodia* (including *Diodella*) into two indehiscent one-seeded cocci. *Borreria* capsules separate into two one-seeded halves, with each half longitudinally dehiscent on the inner face. *Spermacoce* capsules divide slightly unequally, the common partition remaining attached to one half, which thereby remains indehiscent, while the second half is open on the inner face. *Ernodea* forms a thin-fleshed two-seeded indehiscent berry.

Mitracarpus is sharply distinguished from these members of the tribe *Spermacoceae,* as well as from all other Rubiaceae, by the presence of capsules that open by circumscissile dehiscence, exposing the two single-seeded locules. The detached distal end of a matured fruit, with its four persistent calyx lobes, two very much larger than the others, resembles a fancied child's cap, sporting two prominent donkey ears. The seeds are 1 mm long, each bearing an x-shaped groove in place of the longitudinal sulcus of the typical rubiaceous "coffee-bean" seed; this groove divides the placental surface of the seed into four rounded and nearly equal lobes.

In the continental United States *Mitracarpus villosus* has been known previously from southern Texas (Correll & Johnston, 1970, as *Mitracarpum hirtum*). In the West Indies and in Central and tropical South America it is widespread and often weedy. It has now appeared in central peninsular Florida: dry open sandy roadside, along Fla. 40, near Central Lookout Tower, Ocala National Forest, 24 miles east of Ocala, Marion County. *L. Baltzell* 4494, 5 Nov, 1972. (FLAS 118631, 118632). The population consists of many thousands of individuals, extending for several miles on the Citronelle sand of a pipeline right-of-way through sand pine (*Pinus clausa*) scrub. A second collection, *Ward* 8870, has been distributed to the following institutions: BH, BM, C, FSU, GA, GH, LAF, LSU, MISSA, MO, NCU, NLU, NY, US, USF, VDB.

The plants are erect annuals, to 5 dm in height, and are usually sparingly branched. The stems are very lightly pubescent, and the leaves, especially on the margins and the veins beneath, are scabrous. The leaves are subsessile, narrowly ovate and entire, with the veins deeply impressed above. Each node above the mid-point of the stem bears a dense glomerulate inflorescence; these develop in an upward succession from July into November. The flowers are very small, white, 4-petaled, with scarcely exserted anthers, and give rise to numerous capsules with the persistent dimorphic calyx lobes and circumscissile dehiscence characteristic of the genus. Without careful examination the plants may readily be passed as exceptionally tall and erect specimens of *Borreria laevis* (Lam.) Griseb., a common species of somewhat moister habitats.

The Ocala population represents one of an aggregation of forms that have been given such additional names as *Mitracarpus hirtus* (L.) DC., *M. rude* Benth., *M. diffusus* (Willd.) Cham. & Schlecht., *M. bakeri* Urban, and *M. simplex* Rusby. There seems to be no present way to determine whether this grouping represents one species or more than one. Such authorities as Schumann (1888, 1891) and Standley (1930, 1931a, 1931b) have chosen to

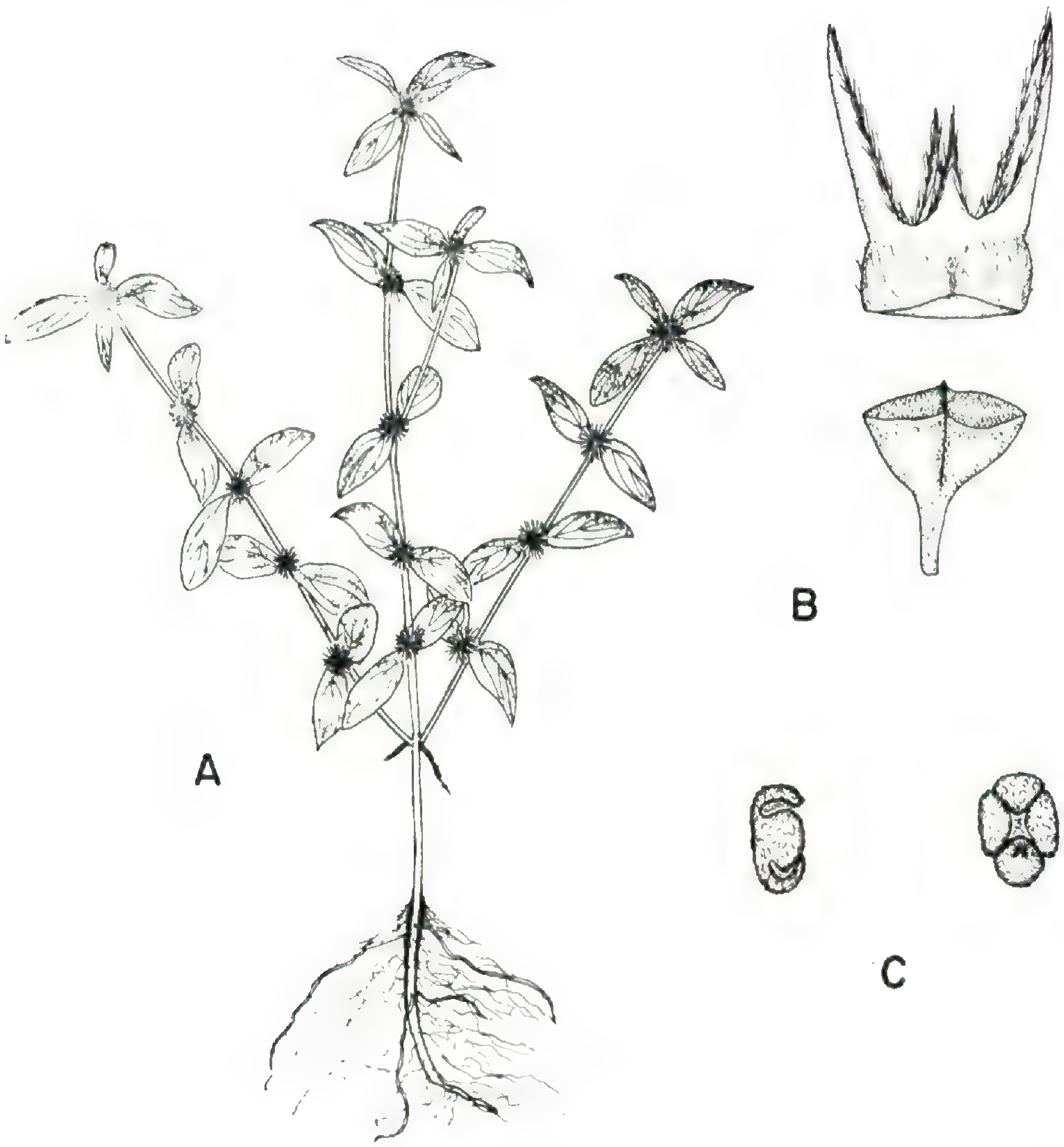

Fig. 1. *Mitracarpus villosus.* A, habit × ¼; B, capsule, with circumscissily dehiscent lid bearing four persistent calyx lobes × 10; C, seed, in side view (left) and placental view (right) × 10.

consider the complex as consisting of a single species, while Steyermark (1972) has strongly indicated that in Venezuela *M. diffusus*, at least, deserves recognition. But in any event the Florida collections do not appear separable from the widespread entity of the New World tropics.

Although there are representations to the contrary, the correct name of this plant is *Mitracarpus villosus* (Sw.) DC. (1830), with the basionym *Spermacoce villosa* Swartz (1788). The original account was written by Swartz fol-

lowing several years of active field work in Jamaica, and his description, although brief, is appropriate for the present species and is supported by specimens examined by Rendle (1936) and others.

But *Mitracarpus hirtus*, of varying authors, has been used with almost equal frequency. Although not fully stated by its advocates, a case may be made that this combination is prior and correct. The earliest name attributed to this group is *Spermacoce hirta* Linnaeus (1762), used in describing a plant from Jamaica. Swartz's 1788 description of *S. villosa* Sw., although also based upon Jamaican plants, was independent. In 1791 Swartz described still a third Jamaican collection, again using *Spermacoce hirta;* although he referred to Linnaeus in noting that this latest species had been (in translation) "accidentally confused and mixed" by Linnaeus with Swartz's earlier *S. villosa,* Swartz's 1791 description was wholly original and it is conceivable that he thought of his usage of *hirta* as being new. DeCandolle in 1830 made the combination *Mitracarpus hirtus* (as *hirtum*), basing his name on *S. hirta* Swartz, not on *S. hirta* Linnaeus.

If *Spermacoce hirta* Swartz were indeed to be taken as a new name, then DeCandolle's *M. hirtus* would be illegitimate since based on a later homonym, and the correct name would be *M. villosus* (Sw.) DC. But if it were seen that DeCandolle's citation of Swartz was an indirect reference to Linnaeus, then *M. hirtus* (L.) DC. would be legitimate and prior. Fortunately, this decision is moot, for the morphology of the types and the particulars of the descriptions provide a definite answer.

Specimens of at least two entirely different rubiaceous genera are involved. Linnaeus's original description of *Spermacoce hirta* was moderately lengthy but wholly ambiguous, and the surviving specimen in the Linnaean Herbarium (125.4) seems in microfiche to be immature; nevertheless the prominent petioles and other characteristics of the Linnaean specimen, as described by Steyermark (1972),

are definitely not those of the plant known as *M. villosus.* Swartz in 1791 gave a full and detailed description of his own *S. hirta*, and characteristics of the stamens ("exserta"), the calyx ("4-dentatus, brevissimus"), and the seeds are in sharp contradiction with those of *M. villosus;* indeed, Swartz's 1791 plant is most suggestive of *Hemidiodia ocymifolia* (Willd.) Schum. in Mart., a tropical adventive to which Linnaeus's specimen may also belong. Thus, whatever the date and authorship attributed to *M. hirtus*, its irrelevance to the problem at hand leaves *M. villosus* (Sw.) DC. without challenge.[1]

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[1]In a publication received too recently for inclusion in the above discussion, B. Verdcourt (Kew Bull. 30:317-322. 1975) discusses in full detail this matter of the correct name for the common species of *Mitracarpus*. He is personally inclined to the view that DeCandolle's reference to Swartz was indeed an indirect but clear reference to *Spermacoce hirta* L. and that the correct name should be *M. hirtus* (L.) DC. He saw the chain of attribution as running from DeCandolle's citation of *Spermacoce hirta* Sw., through Swartz's reference to Reichard's *Systema Plantarum* (1:291. 1779), to Browne's *Civil and Natural History of Jamaica* (141. 1756), and thence forward in time to Linnaeus (1762).

Fortunately the improbabilities of this indirect attribution need not be argued, for Verdcourt reluctantly defers to the judgment of his consultants, the skilled Linnaean scholars J. E. Dandy and W. T. Stearn, who maintain that DeCandolle's phrasing expressly excluded the type of *Spermacoce hirta* L., a circumstance that would compel the use of *Mitracarpus villosus* (Sw.) DC.

Verdcourt makes two other points germain to the present discussion, both less than incontestable, but in the opinion of the present writer, probably valid. First, he believes the specimen upon which *Spermacoce hirta* L. is based *not* to be the one discussed above and by Steyermark (1972), but to be a second sheet in the Linnaean Herbarium (125.8). Linnaeus wrote "hirta" upon his first sheet (125.4), suggesting to Steyermark and the present writer that this specimen represented his type, while he wrote "hispida" upon the second (125.8), a reference to *Spermacoce hispida* L., an Asian species in no other way involved with this problem. That Linnaeus labeled this second sheet in careless haste is implied by the facts that (1) the specimen is a true *Mitracarpus*, apparently the common New World species, (2) *Spermacoce hispida* L. is not known in Jamaica or elsewhere in the New World, and (3) the sheet also bore in Linnaeus's

Mitracarpus has been spelled in two ways. Schultes, who established the genus in 1827, spelled the name *Mitracarpum* in his text. Such authors as Schumann (1888, 1891), Urban (1913), Standley (1930, 1931a, 1931b), Rendle (*in* Fawcett & Rendle, 1936), Alain (1962), Hepper (*in* Hutchinson & Dalziel, 1963), Adams (1972), and Steyermark (1972), interpreted the genus to be masculine, and spelled it *Mitracarpus*. But Chamisso & Schlechtendal (1828), DeCandolle (1830), Grisebach (1864), and Hooker (*in* Bentham & Hooker, 1873), as well as such recent writers as Verdcourt (1958) and Correll & Johnston (1970), have seen the genus as neuter, and have used *Mitracarpum*.

Dr. William J. Dress has adroitly resolved for the writer this question of generic gender and spelling. He notes that the original text by Schultes mentions the genus only in the accusative case (p. 120), and thus Schultes's *Mitracarpum* could be either neuter or masculine since the accusative ending for both would be the same. But in Schultes's index (p. 399), a listing in the nominative case, Dr. Dress observes the entry to be *Mitracarpus*. Since the original author's intent as to gender thus seems to be

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hand a "3" which was the species number he assigned to *S. hirta* L., and a "Br" by which he noted he had obtained it from Patrick Browne who had collected only in Jamaica. This second sheet, if seen as the type, as now appears reasonable, makes the decision critical as to whether DeCandolle was indirectly referring to Linnaeus's *Spermacoce hirta*.

Second, Verdcourt has called attention to the illegitimacy of *Mitracarpus villosus* (Sw.) Cham. & Schlecht., a combination used by Steyermark (1972) and others including the present author. Chamisso & Schlechtendal (1828) did antedate DeCandolle by two years, and DeCandolle credited them with the combination, but in their treatment of *Spermacoce villosa* Sw. they merely recorded its placement in *Mitracarpus*, without indicating that a particular combination was to be used, a contravention of Art. 33 of the International Code. Specimens of *Ward* 8870 bearing this invalid combination have been distributed and should now be corrected to *Mitracarpus villosus* (Sw.) DC.

without ambiguity, this latter spelling should be used, and the epithets should of course agree.[2]

The writer is grateful to Dr. Dress for assistance with orthographic matters, to Miss Vicki Rosario for the illustration, and to Mr. and Mrs. L. M. Baltzell, Leesburg, for their indefatigable efforts to understand and collect the flora of central Florida. This paper is Florida Agricultural Experiment Journal Series No. 5504.

LITERATURE CITED

ADAMS, C. D. 1972. Flowering Plants of Jamaica. Mona, Jamaica. 848 pp.

ALAIN, H. 1962. Flora de Cuba. Rio Piedras. 5:141-145.

CANDOLLE, A. P. DE. 1830. Prodromus Systematis Naturalis Regni Vegetabilis. 4:572.

CHAMISSO, A., & D. SCHLECHTENDAL. 1828. De plantis in Expeditione Speculatoria Romanzoffiana observatis. Linnaea 3:363.

CORRELL, D. S., & M. C. JOHNSTON. 1970. Manual of the Vascular Plants of Texas. Texas Research Foundation, Renner. 1881 pp.

GRISEBACH, A. H. R. 1864. Flora of the British West Indian Islands. London. 789 pp.

HEPPER, F. N. 1963. *In* J. Hutchinson & J. M. Dalziel. Flora of West Tropical Africa. 2:222.

HOOKER, J. D. 1873. *In* G. Bentham & J. D. Hooker, Genera Plantarum. 2:146-147.

LINNAEUS, C. 1762. Species Plantarum, ed. 2. p. 148.

RENDLE, A. B. 1936. *In* W. Fawcett & A. B. Rendle. Flora of Jamaica. 7:127-128.

SCHULTES, J. A. 1827. Mantissa in Volumen Systematis Vegetabilium. 3:210.

[2]After the present manuscript was accepted for publication the writer was delighted to come upon an elegant solution of this same problem, by W. R. Anderson (Taxon 20:643. 1971). From the text alone Anderson reasoned that Schultes's use of "Mitracarpum" could have been either masculine or neuter, but not feminine, while his use of the modifying participle "crescentem" ("growing") could have been either masculine or feminine, but not neuter. Thus Anderson was led, by a logic parallel to but independent of Dress's, to the identical conclusion, that Schultes's genus was thought of by its author as masculine. It would seem now beyond dispute that this genus in the nominative should be spelled *Mitracarpus!*

SCHUMANN, K. 1888. *In* K. F. P. von Martius. Flora Brasiliensis. 6(6):84.

———. 1891. *In* A. Engler & K. Prantl. Die Naturlichen Pflanzenfamilien. 4(4):146.

STANDLEY, P. C. 1930. The Rubiaceae of Colombia. Field Mus. Nat. Hist. Bot. Ser. 7:1-176.

———. 1931a. The Rubiaceae of Bolivia. Field Mus. Nat. Hist. Bot. Ser. 7:253-340.

———. 1931b. The Rubiaceae of Venezuela. Field Mus. Nat. Hist. Bot. Ser. 7:341-486.

STEYERMARK, J. A. 1972. The Botany of the Guayana Highland — Part IX. Mem. New York Bot. Gard. 23:777-784.

SWARTZ, O. 1788. Nova Genera et Species Plantarum seu Prodromus. p. 29.

———. 1791. Observationes Botanicae. p. 45.

URBAN, I. 1913. Symbolae Antillanae. 7:551-553.

VERDCOURT, B. 1958. Remarks on the classification of the Rubiaceae. Bull. Jard. Bot. Bruxelles. 28:209-290.

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AN ACCOUNT OF SOME NEOTROPICAL TARAXACUM SPECIES

A. J. Richards

The genus *Taraxacum* (Lactuceae-Compositae) is a highly successful group of perennial herbs which, although centered in Eurasia, are native in five continents. The major of the 2000-odd species are polyploid seed-apomicts, and, being genetically invariable, can be regarded as 'microspecies.' Although the species are rightly regarded as taxonomically 'critical,' this is largely due to the considerable phenotypic plasticity displayed, so characteristic of genetically invariable units. A careful examination of well-grown material during the main flowering period at temperate latitudes will rarely lead to taxonomic difficulty (Richards, 1972). However, abnormal phenotypes are adopted at other times of year, and this phenomenon creates particular difficulties in tropical regions where *Taraxacum* apparently displays no marked flowering period and thus exhibits even more plasticity than is usual.

Whereas the native *Taraxacum* species of North America are relatively well-known, those of neotropical regions, south of the United States, have been largely ignored. Up till now, only eight species have been described: *T. magellanicum* Comm., *T. melanocarpum* Dahlst., *T. gillesii* Hooker & Arnott, *T. ibari* Phil., and *T. rhusiocarpum* Dahlst., all from Tierra del Fuego, and *T. andinum* Dahlst., from the southern Andes, belong to the section *Arctica* Dahlst. em. Richards, a circum-arctic section with a number of North American species; *Taraxacum mexicanum* DC, from Mexico above 2000 m, and *T. fernandezianum* Dahlst., from the island of Juan Fernandez, are closely related and have heretofore not been classified. It is noteworthy that no species in the circum-arctic section *Ceratophora* Dahlst., of which about 50 species have been described from North America, mostly in the Arctic, have been recorded from Central and South America.

In the present paper, nine additional native species are reported from the neotropical regions. These are placed with *Taraxacum mexicanum* and *T. fernandezianum* in a new section *Mexicana*.

It has been recognised for some time that some species in the European sections *Vulgaria* Dahlst. (*Taraxacum officinale* Wigg. s.l.) and *Erythrosperma* (H. Lindb. f.) Dahlst. (*T. levigatum* (Willd.) DC or *T. erythrospermum* Andrz. s.l.) are adventive in many regions of the world, including the American continent. American taxonomists have invariably used these aggregate species names, and the only account of the microspecies adventive in America concerns the *Erythrosperma* in North America (van Soest, 1958). During the present study, I have examined specimens of a number of European species adventive in Central and South America, and these are also enumerated.

MATERIAL STUDIED

During the course of this study, I have seen some 300 herbarium sheets of *Taraxacum* from neotropical regions. These include the collections of the United States National Museum, Smithsonian Institute, Washington (US); the New York Botanic Garden (NY); the University of Michigan Herbarium, Ann Arbor (MICH); the Nacional Herbario, Universidad Nacional de Mexico (MEXU); the Rijksherbarium, Leiden (L); the Reading University Herbarium (RU); the Herbarium of the Royal Botanic Gardens, Kew (K); the Botaniska Riksmuseet, Stockholm (S); Escuela Nacional de Ciencias Biologicas, Mexico (IPN); and the Herbarium of the Royal Botanic Gardens, Edinburgh (E). I should like to thank the respective authorities for allowing access to this material.

In addition, I have cultivated *Taraxacum fernandezianum* from two gatherings of seed, by Dr. S. R. J. Woodell from the Castle Hotel, Bermuda; and by Professor J. L. van Soest from Arrayan, Chile.

SYSTEMATIC ACCOUNT

Taraxacum sectio Mexicana A. J. Richards, sect. nov.

Plantae mediocres vel parvae pilosae. *Folia* lanceolata vel spathulata, lobata vel subintegra, griseo vel obscuro-viridia. *Scapi* subtenues erecti, interdum valde lanati et breves. *Squamae exteriores* parvae, ad 7-10 mm longae, saepe 4-5 mm, lanceolatae vel ovato-lanceolatae, in parte vel toto scariosae, virides vel griseo-brunneae, ecorniculatae, erectae usque recurvatae. *Capitulum* subparvum, ad 35 mm diametro, flavum usque citrinum, polliniferum vel epolliniferum. *Achenium* stramineum usque griseo-brunneum, parvum, ad 3.0 mm longum (pyramide exclusa), in pyramidem 0.5-1.2 mm cylindricam subabrupte abiens; rostrum tenue, 5-7 mm longum. *Pappus* sordide albus usque pallide stramineus. Semper? agamospermae. Plantae neotropicae inter 2000-4000 m altitudinis. Type species: *T. mexicanum* DC.

The section *Mexicana* includes 11 closely related species of *Taraxacum*, only two of which (*T. mexicanum* and *T. fernandezianum*) have been described previously. All are apparently confined to Central and South America, the West Indies and Bermuda. Three species seem to be restricted to Mexico, and a further three to Central America. These six species occur in rather natural associations between 2000 and 4000 metres. A further two species are found in discrete areas of South America, one in Venezuela and the other on the borders of Chile and Peru. Both are plants of high altitude. In addition, one species is widespread in South America, including some lowland stations in which it may be adventive, while *T. fernandezianum* is mostly known from low altitude localities and is very widespread, being recorded from Juan Fernandez, Chile, Peru, Brasil, Argentina, the West Indies, Central America and Bermuda. It may be adventive in some or most of these areas, and it is not clear where it is native. One species seems to be endemic to Jamaica.

The section is characterised by small, often scarious exterior bracts (in some cases among the smallest known in the genus) that characteristically contrast with the darker involucre of interior bracts, and by small achenes with a cylindrical cone, a rather short but fine beak, and a distinctly discoloured pappus that in many cases may be yellowish. No other neotropical *Taraxaca* have a discoloured pappus. Those with small exterior bracts either have bracts that are not scarious and are usually corniculate (section *Erythrosperma*), or are dark and adpressed to the involucre (section *Arctica*). Cylindrical cones to the achenes are otherwise found in the section *Erythrosperma*, in which the achenes are, however, usually reddish. The section *Vulgaria* are relatively gross plants with exterior bracts exceeding 7 mm, and with a short conical cone to the achene.

The relationships of the section *Mexicana* are of great interest. Superficially, they resemble most small members of the section *Vulgaria*, but the small bracts and the shape of the achene is more reminiscent of the section *Erythrosperma*. These are both largely apomictic groups from Europe of an 'advanced' type (Richards, 1973). However, the section *Mexicana* is more primitive, both in the scarious exterior bracts and especially in the discoloured pappus, which is rarely found in *Taraxacum* and is almost confined otherwise to primitive sexual species from western Asia. There is no conceivable link with the other two native groups of *Taraxaca* in America, the *Arctica* and *Ceratophora*. If one was to imagine a hybrid between these sections (some *Arctica*, including *T. magellanicum* are sexual), it might resemble the *Mexicana* in some ways, but the discoloured pappus and cylindrical cone to the achene would be difficult to explain, as these do not occur in either section. However, any alternative explanation would invoke either a direct link with South-West Europe, or widespread extinction of *Mexicana* types from large areas of Asia and North America. In short, the origin of the *Mexicana*, and its relationships are a mystery.

A KEY TO SECTIONS AND SPECIES OF NEOTROPICAL TARAXACA

1. Plant robust; exterior bracts exceeding 8 mm, spreading to recurved, neither scarious nor corniculate; rostrum exceeding 8 mm; pappus white. ...... section *Vulgaria*.
1. Plant smaller, more delicate, occasionally robust; exterior bracts rarely exceeding 8 mm, adpressed to recurved, often scarious or corniculate; rostrum 5-13 mm; pappus white or discoloured. .... 2.
   2. Plant small and delicate with dissected leaves; exterior bracts not mostly scarious or membranous, usually corniculate; achenes usually reddish with a cylindrical cone; rostrum exceeding 7 mm; pappus white. .... section *Erythrosperma*.
   2. Plant small to robust; exterior bracts often mostly scarious, never corniculate; achenes rarely reddish, cone cylindrical or poorly differentiated; rostrum 5-13 mm; pappus white or discoloured. .... 3.
      3. Plant delicate and usually rather short with glabrous leaves; exterior bracts not membranous, although often with a scarious border, erect to adpressed; achenes fusiform, cone scarcely differentiated; rostrum not exceeding 6 mm; pappus white (section *Arctica*). .... 4.
      3. Plant less delicate, leaves usually with some indumentum; exterior bracts thin, often scarious or membranous, paler than interior bracts, erect to recurved; achenes abruptly narrowed above to form a cylindrical cone; rostrum 5-13 mm; pappus usually discoloured, sometimes yellowish (section *Mexicana*. .... 7.
         4. Pollen absent; achenes reddish. .... 15. *T. rhusiocarpum*.
         4. Pollen present; achenes lacking reddish hue. .. 5.
            5. Leaves narrow, subentire to lobate; exterior bracts rarely exceeding 3 mm in width, with a broad scarious border. .... 12. *T. magellanicum*.
            5. Leaves wider, even ovate, deeply dissected; exterior bracts commonly exceeding 3 mm in width, with a narrow border, or concolorous. .... 6.

6. Scapes shorter than leaves at flowering; exterior bracts concolorous. . . . . 14. *T. gillesii.*
6. Scapes usually exceeding leaves at flowering; exterior bracts with a narrow white or rose-coloured border. . . . . 13. *T. andinum.*
  7. Exterior bracts exceeding 8 mm; achenes 3.5 mm; rostrum 10-13 mm. (C. America). . . . . 11. *T. tenejapense.*
  7. Exterior bracts less than 7 mm; achenes less than 3.2 mm; rostrum less than 9 mm. . . . . 8.
    8. Petioles narrow, unwinged, rose; involucres narrow (to 10 mm), blackish. (Chile, Peru). . . . . 8. *T. cuzcense.*
    8. Petioles variable; involucres usually more than 10 mm wide, never blackish. . . . 9.
      9. Leaves lacking clearly defined lobes; exterior bracts 1 mm in width. . . . . 10.
      9. Leaves lobate; exterior bracts usually 1.5-2 mm in width. . . . . 11.
        10. Leaves spathulate, green, not very dentate; exterior bracts with a narrow white border. (C. America, Haiti). . . . . 5. *T. spathulatum.*
        10. Leaves narrowly lanceolate, grey-green, dentate throughout; exterior bracts scarious throughout. (widespread). . . . . 2. *T. fernandezianum.*
          11. Scape not exceeding 50 mm at flowering, often almost absent, woolly. (C. America). . . 1. *T. mexicanum.*
          11. Scape usually longer at flowering, sometimes pilose but never woolly. . . . . 12.
            12. Leaf-lobes strongly recurved with a convex distal margin. . . . 13.
            12. Leaf-lobes patent or slightly recurved; distal margin not markedly convex. 14.

13. Leaf-lobes dentate; exterior bracts erect, 4 mm, submembranous. (Jamaica). . . . . 4. *T. unguilobifrons.*

13. Leaf-lobes mostly entire; exterior bracts spreading, 5 mm, not membranous. (Venezuela). . . . . 9. *T. craspedotoides.*

14. Exterior bracts erect, 4 mm, submembranous; leaves pale green with dentate triangular lobes. (Mexico). . . . . . 10. *T. disseminatoides.*

14. Exterior bracts patent or recurved, 4-6 mm, not membranous; leaves darker. . 15.

15. Plant robust; exterior bracts recurved, 6 × 2 mm; involucre dark green. (S. America). . . . . 3. *T. subspathulatum.*

15. Plant less robust; exterior bracts patent, 4-5 × 1.5 mm; involucre not dark. . . . . 16.

16. Leaf-lobes deltoid; exterior bracts with a clear white border; achenes 3.0 mm. (Mexico). . . . . 7. *T. calocephaloides.*

16. Leaf lobes triangular, acute; exterior bracts with an indistinct border; achenes 2.5 mm. (C. America, Haiti). . . . . . 6. *T. argutifrons.*

1. **Taraxacum mexicanum** De Candolle. Prod. Suppt. Not. 7:146 (1838).

Plant small to medium-sized, glabrous except at the base and on the scapes. Leaves 30-150 mm, decumbent to ascending, broadly lanceolate or subspathulate, lobate. Lateral leaf-lobes usually three, short, acute, triangular, entire or acuminate-dentate; terminal leaf-lobe poorly demarcated, short, obtuse; petiole short, winged, dull rose-pink. Scapes few, erect, usually very short (to *50 mm* and often *almost sessile*) at flowering, elongating to 200 mm in fruit, at first *densely lanate,* later glabrescent. Exterior bracts *erect, 5 × 1.5 mm,* olive-green with a *pale margin.* Capitulum 20-25 mm in diameter, deep yellow; ligules bearing purple stripes; style and stigma dirty green, with or without pollen. Achene straw-brown, 2.6 mm (excluding the cone), tuberculate at apex, with *a short* (*0.5 mm*) subcylindrical cone. Rostrum *7 mm, thin.* Pappus discoloured.

Taraxacum mexicanum is a widespread and apparently locally common species above 2000 m in Mexico. It is immediately known by the very short and woolly scapes at flowering. In addition, the short cone and rather long rostrum to the achenes and the short, broad, erect bracts with pale margins are distinctive.

The original description in De Candolle is minimal, but the phrase "scapis folio brevioribus, sparse subvillosis," although an understatement, is diagnostic. I have seen a photograph of the specimen from De Candolle's herbarium at Geneva, which undoubtedly refers to this taxon (mountains around Mexico City, Berlandier). The description in Handel-Mazzetti (1907:75-76) is much more complete and forms a satisfactory diagnosis. Handel-Mazzetti gives five localities, all in Mexico. In addition I can add:

REPRESENTATIVE SPECIMENS: **Mexico:** CHIAPAS: San Cristobal las Casas, 7100′, 14.2.1966, *R. M. Laughlin* (NY). COAHUILA: Parras de la Fuente, Rincon del Monteso, *D. B. Ward* 5748 (MICH). DISTRITO FEDERAL: Canada de Contreras, 3100 m, *C. Vazquez* 20 (MEXU); Canada de Contreras, Cuarto Dinamo, 3100 m, 21.3.1965, *H. Hernan-*

dez (MEXU); Barranca de Solis Grande, Lomas Atlas, 2400 m, *L. Huerta* M. 18 (MEXU). DURANGO: 5 miles north of railway at Coyotes, 2400-2500 m, *J. H. Maysilles* 8282 (MICH); El Carazon, *P. G. Russell, M. J. Souviron* 107 (US). HIDALGO: Puente de Tasquillo, *L. Gonzalez Quintero* 2020 (MEXU); Ixmiquilipan, 9 km north of Orizabita, 2500 m, *L. Gonzalez Quintero* 2593 (MEXU); Los Pescados, Cofre de Perote, 10,700′ *E. K. Balls* 4585 (US). MEXICO: 4 km north of Atizapan, 2350 m, 11.6.1967, *A. Vargas* (N. MEXU); Texcoco, Ahuehuete, 2250 m, 25.11.1951, *E. Matuda* (NY); Nevada de Toluca, 4.8.1962, *L. Huerta* (M. MEXU); Chimalhuacan, 2300 m, 28.7.1964, *A. Castro* (MEXU); Nevada de Toluca, Ojos de Aqua, 12,800′, *E. K. Balls* 4105 (US); Llano grande, 3000 m, 10.7.1951, *E. Matuda* (NY). TAMAULIPAS: reservoir of Miquihuana, 10.7.1949, *Stanford, Taylor and Lauber* (MICH); 5 km north of Atizapan, 2400 m, 6.9.1964, *A. Villamar* (C. MEXU); Chemalhuacan, 2250 m, 7.6.1964, *A. Mendoza* (MEXU); Penas Cuates, north-west of Ixtaccihuatl, 3500 m, *Rzedowski* 21809 (MEXU); Santa Cruz Cuahtenco, La Vereda, 2900 m, *L. Hilario* A. 13 (MEXU); Chalco, Camacho, 2750 m, 11.9.1966, *Fagoaga* (MEXU). PARAJE PROVINCIAL: Popocatepetl, 11,500′, *E. K. Balls* 4183 (US). PUEBLA: on route 150, 17 m east of Puebla, *R. M. King* 2271 (MICH); San Juan Citlaltepec, Lago de Zanpango, 5.6.1966, *V. Velaquez* (MEXU). TEMASCALTEPEC: Cumbre-Gavia, 1936, *G. B. Hinton* (NY, US). VERACRUZ: Boca del Monte, *E. W. Nelson* 226 (US); Orizaba, Lomogrande, 9200′, 27.4.1938, *E. K. Balls* (K).

2. **Taraxacum fernandezianum** Dahlstedt apud C. Skottsberg. Nat. Hist. Juan Fern. and Easter I. 2:226 (1922).

Plant small to medium-sized, subglabrous, or pilose on the mid-ribs. Leaves 70-150 mm, decumbent to ascending, *grey-green*, lobate, usually *indistinctly* so, or frequently *without lobes but deeply and irregularly dentate;* leaf-lobes 2-4, short, recurved; terminal leaf-lobe obtuse or ± acute, entire; petiole unwinged, dull purple or occasionally green. Scapes ascending or erect, exceeding leaves at flowering, pilose, but scarcely lanate at first, becoming glabrescent. Exterior bracts patent, or somewhat recurved, narrowly lanceolate, 5 × 1, pale, olive-green, or sometimes brownish-red, and ± scarious. Capitulum 25-35 mm in diameter, yellow; ligules bearing dark or grey-violet stripes; style yellow, stigma yellow at first, becoming dark in a dried condition; pollen usually present (Dahlstedt says it can be

absent). Achenes straw-brown to light warm brown, 3.0-3.2 mm (excluding cone), spinulose above; cone cylindrical, 0.8 mm. Rostrum slender, 7-8 mm; pappus off-white. 2n = 24. Agamospermous.

Taraxacum fernandezianum was first described by Dahlstedt from the islands of Masafuera and Masatierra, Juan Fernandez (S). Since then it has been found from sea-level to 3000′ throughout much of Central and South America, the West Indies and Bermuda. It is by far the most widespread member of the group, and the most catholic in habitat requirement, although most stations seem to be on disturbed ground near the coast. Only in this species, which seems to have been the only one in cultivation (at Leiden and Newcastle) do we have evidence of chromosome number and apomictic behaviour. However, all other species show characters of apomictic behaviour (good seed-set, irregular pollen, or lack of pollen), and it is probable that all members of the section are polyploid (most probably triploid) apomicts.

Taraxacum fernandezianum is best diagnosed by its leaf shape, which is narrowly oblong-spathulate, with many indistinct short lobes and is consistently dentate from apex to petiole; the leaves are a characteristic grey-green. The exterior bracts are typical for the section, being small, narrow and largely scarious. The achene has the small size and cylindrical cone of the section.

In addition to the type localities on Juan Fernandez, I can add:

REPRESENTATIVE SPECIMENS: **Bermuda:** Agaris, *F. S. Collins* 314 (US); The Castle Harbour Hotel, 12.1969, *S. R. J. Woodell*, as seed (OXF), $2n = 24$; Flatts, *F. S. Collins* 314 (US). **Haiti:** Don, Citadel top, 400 m, *E. C. Leonard* 8626 (US); Funds Varettes, Mission, *E. C. Leonard* 3634 (US); Mean Rabel, 2.3.1929, *E. C. and G. M. Leonard* (US); Massif de la Pelle, Petionville, M. Tranchard, 1640 m, 2.8. 1924, *E. L. Ekman* (US); Morues des Commissaires, 1600 m, *L. R. Holdridge* 899 (US). **Honduras:** MORAZA'N: Montana La Tigra, San Juancito, 200 m, *A. Molina* 10117 (US). **Dominican Republic:** Constanza, 17.5.1959, *J. J. Jiminez* (US). **Guatemala:** Tabz, 1905, *W. A.*

Kellerman (US). **Costa Rica:** San Jose, San Pedro de Mantes de Oca to Curnidibat, 1200 m, *P. Standley* 32820 (US). **Mexico:** DISTRITO FEDERAL: Deserto de Leon, 2400 m, *E. Matuda* 18803 (US); Monelia, 11.1889, *A. Duges* (US); Querotoro, *G. Arsène* 10535 (US). **Brasil:** CURITIBA: Rua Cel Dulcidio, 820 m, *J. C. Lindemen and J. H. de Haas* 487 (US). SANTA CATARINA: Porto Uniao, Rio Liguaco, 750 m, *L. B. Smith and R. R. Reitz* 8794 (US). **Argentina:** EL CARMEN: prope Salta, 9.10.1901, *R. E. Fries* (US); Neuquem, Quebrada de Tiu-Tiu, *R. Maldorato* 67 (L). **Chile:** Arrayan, 29.3.1967, *J. L. van Soest* (L and OXF), $2n = 24$; Santiago, El Golf, 1.4.1967, *J. L. van Soest* (L). **Peru:** HUANUCO: Carpish Pass, Tingo Maria to Lima, 2750 m, *H. A. Allard* 21012 (US); Oroya, 10,000-13,000′, s.n., no date, *A. S. Kalenborn* (US).

3. **Taraxacum subspathulatum** A. J. Richards, sp. nov. Holotype: Argentina: Tucumán: Villa Vougues, 1000 m, *S. Venturi* 1470 (US).

Planta mediocris. *Folia* olivaceo-viridia, ascendentes 70-130 mm, lobata, spathulata. Lobi laterales 1-3, recurvati, angusti, in margine superiore sat convexi, dentati; lobus terminalis paulo distinctus, obtusus, dentatus. *Petiolus* sordide roseus, exalatus vel, in petiolis brevibus, alatus. *Scapi* breves per anthesin, deinde elongati, crassi, pilosi saepe dense. *Squamae exteriores* recurvatae, 5-6 × 2 mm, obscuro-virides, vel purpurascentes, emarginatae, ecorniculatae. Involucrum crassum, subnigrum. *Capitulum* c. 35 mm diametro, flavum; ligulae stria extus grisea notatae; stylus stigmaque siccum subnigrum, valde polliniferum. Achenium stramineo-brunneum, 2.5 mm, tuberculatum, in pyramidem subconicam 0.5 mm subabrupte abiens. *Rostrum* 7 mm. *Pappus* sordide albus. E. sectione *Mexicana*.

REPRESENTATIVE SPECIMENS: **Argentina:** TUCUMAN: Tafi, Siambou, 1200 m, *S. Venturi* 3936 (US); Chile cito, 1000-1200 m, 4.1960, *L. L. W. van Soest* (L). **Chile:** SANTIAGO: 21.4.1967, *J. L. van Soest* (L); Valparaiso, Gargen Suizo, Las Zonas, *J. W. Harshberger* 1050 (US). **Peru:** Oroya, 10,000-16,000′, *A. S. and H. Kalenborn* 1918 (NY). **Bolivia:** Cercado. Valle de Cochabamba, 2570 m, 5.4.1966, *R. F. Steinbach* (NY); Valle de Cochabamba, 2600 m, 24.11.1928, *J. Steinbach* (NY, K). **Juan Fernandez:** Masatierra, Cumberland Bay, 23. 12. 1954, *C. Skottsberg* (L).

Taraxacum subspathulatum is a distinctive species with dark broad involucres and broad spathulate leaves with recurved leaf-lobes. It can only be confused with *T. unguilobifrons* among the *Mexicana*, from which it is readily distinguished by having spathulate leaves and larger darker involucres. It occurs in a different region from most other *Mexicana* species, being apparently restricted to Central South America, Bolivia and Juan Fernandez. Also, it is not typical for the section Mexicana, being rather robust in floral features for that section.

4. **Taraxacum unguilobifrons** A. J. Richards, sp. nov. Holotype: Jamaica: Farm Hill, *C. R. Orcutt* 3280 (US).

Planta mediocris-subalta. *Folia* olivaceo-viridia, ascendentia usque suberecta, 100-150 mm, angusta, lobata. Lobi laterales (2)-3-(4), breves, recurvati, hamati, in margine superiore valde convexi, dentati; lobus terminalis brevis, hamatus; petiolus angustus exalatus, purpureus. *Scapi* folia excedentes, purpurei, araneoso-pilosi sub involucro. *Squamae* exteriores patentes vel subrecurvatae, submembranaceae, 4 × 1.4 mm, pallide virides, vel rubescentes, emarginatae, ecorniculatae. *Capitulum* 15-20 mm diametro, citrinum; ligulae stria cano-violacea extus notatae; stylus stigmaque obscurum, polliniferum. Achenium ignotum. E sectione *Mexicana*.

REPRESENTATIVE SPECIMENS: **Jamaica:** Cuichona. 4900 ft, *W. Harris* 10926 (US, K).

Taraxacum unguilobifrons has characteristically recurved, "hamate" leaf lobes, recalling the European species *T. unguilobum* Dahlst. The only species which can be confused are *T. argutifrons,* with longer, more acute, less hamate lobes, and *T. craspedotoides,* which has entire leaf-lobes, without teeth. Moreover, both these species have green exterior bracts; those of *T. unguilobifrons* are membranaceous, as is the case in *T. disseminatoides* and *T. fernandezianum. Taraxacum unguilobifrons* is at present known only from two sites in Jamaica.

5. **Taraxacum spathulatum** A. J. Richards, sp. nov. Holotype: Mexico: Oaxaca: Distrito del Centro, Acueducto de Xochimilco, 1570 m, *C. Conzatti* 5259 (US).

Planta mediocris, subtenella. *Folia* prasino-viridia, erecta, 80-150 mm longa, spathulata, integra vel sublobata, obtusa; petiolus exalatus, roseus; nervus medianus albus. *Scapi* folia aequantes, virides vel rosei, araneoso-pilosi sub involucro. *Squamae exteriores* olivaceo-virides, interdum purpurascentes, 5 × 1 mm. patentes vel subrecurvatae, anguste albo-marginatae, ecorniculatae. *Capitulum* 20-25 mm diametro, citrinum; ligulae extus stria cano-violacea notatae; stylus stigmaque obscurum, polliniferum. *Achenium* ignotum. E sectione *Mexicana*.

REPRESENTATIVE SPECIMENS: **Mexico:** DISTRITO FEDERAL: Llanos de capilco, Contreras, 3000 m, 19.6.1966, *R. Cruz* (MEXU); MEXICO: Presa de la Concepcion, Tepetzotlan, 2350 m, 5.3.1968, *L. Hilirio* (MEXU); Cerro Gordo, San Juan Teotihuacan, 2700 m, 24.4.1966, *F. A. Villanuera* (MEXU). VERACRUZ: Cofre de Perote, Las Pescados, 10,700′, 24.5.1938, *E. K. Balls* (K). **Colombia:** PUTUMAYO: Valle de Sibundoy, 3 km south Sibundoy, 2000 m, *M. L. Bristol* 601 (US). **Haiti:** Mission, Fonds Varettes, 1000 m, *E. C. Leonard* 3917 (US). **Costa Rica:** Fiacade volcán de Turrialba, 2000 m, *P. C. Standley* (US).

Taraxacum spathulatum is best known by its soft, dull pale green, obtusely spathulate leaves, which are without clear lobes. The involucre resembles that of *T. argutifrons*. It is apparently restricted to mountains in Central America and Haiti.

6. **Taraxacum argutifrons** A. J. Richards, sp. nov. Holotype: Mexico: Charcas, San Luis Potosi Alvarez, *E. Palmer* 180 (US).

Planta mediocris usque subalta. *Folia* ascendentia, 80-180 mm longa, obscure prasino-viridia, lobata. Lobi laterales 3-5, paulo recurvati, acuti, dentati, interdum subhamati; lobus terminalis acutus, triangularis vel deltoideus, vel etiam tripartitus, saepe apiculatus; petiolus exalatus, rubro-violaceus. *Scapi* pauci, ascendentes, araneoso-pilosi. *Squamae* exteriores patentes, 5 × 1.5 mm, olivaceo-virides,

sensim pallide marginatae, ecorniculatae. *Capitulum* 30 mm diametro, citrinum; ligulae sublongae, extus stria cano-violacea notatae; stylus stigmaque obscurum, epolliniferum. *Achenium* brunneo-stramineum (vel subcanum), 2.5 mm longum (pyramide exclusa), tuberculatum ad apicem, in pyramidem subconicam 0.5 mm longum subabrupte abiens. *Rostrum* tenue, 6 mm. *Pappus* subalbus. E sectione *Mexicana*.

REPRESENTATIVE SPECIMENS: **Mexico:** SAN LUIS POTOSI: *A. F. Whiting* 993 (MICH). COAHUILA: Saltillo, *E. Palmer* 769 (US). DISTRITO FEDERAL: Ajusco, 3000 m, *I. Castorena* 66 (MEXU); La Cima, 3000 m, (MEXU). DURANGO: South on road from El Salto to Pueblo Nuevo, 2500-2650 m, *J. H. Maysilles* 7813 (MICH, US). HIDALGO: Sierra de Pachuca, Real del Monte, 2770 m, *J. H. Beaman* 2757 (US); 6 km north of Pachuca, 2900 m, *N. Garcia* R.60 (MEXU); 4 miles south of Jacala, on road to Zimapan, *C. Feddema* 1525 (MICH). MEXICO: Nicholas Romero, 1 km north-west of Cahuacan, 2600 m, *F. Brizuela* V.349 (MEXU); 20 km north-east of Texcoco, 2850 m, 9.6.1968, *J. Vargas* V (MEXU); Fraccionamiento "La Herradura," muncipio de Huixquilucan, 2350 m, *M. A. Hernandez* G.123 (MEXU); Los Pescados, Cofre de Perote, 10,700′, *E. K. Balls* 4585 (US). OAXACA: 12 km north of Ixtlan de Juarez on road to Valle Nacional, 2500 m, *R. M. King* 2015 (MICH); Popocatapetl, *J. N. Rose and R. Hoy* 6067 (US). PUEBLA: Neaskio otlati, 8700′, *J. Weaver* 960 (US); Sierra Madre Oriental, Nuevo Leon, 165 m, *F. G. Meyer and D. J. Rogers* 3803 (US). TAMAULIPAS: Miquihuana, *L. R. Stanford, L. A. Taylor and S. M. Lauber* 2373 (US); 6 km west of Miquihuana, 2940 m, *Stanford, Retherford and Northcraft* 726 (NY); Temascaltepec, Las Cruces, 2250 m, *G. B. Hinton* 1046 (US, NY). **Colombia:** PUTUMAYO: Valle de Sibundoy, 3 k north of San Pedro, 2600 m, *P. J. Chindoy* 192 (US). **Haiti:** Bombardopolis, 610 m, *E. C. Leonard* 13392 (US).

Taraxacum argutifrons is closely related to *T. calcocephaloides*, from which it can be distinguished by the spreading exterior bracts with pale, not white margins, and the darker, smaller achenes with a shorter, less distinct cone. The leaves of the two species are similar, but *Taraxacum argutifrons* can never be said to possess deltoid side lobes, a distinctive feature of *T. calocephaloides*.

It is widespread, and probably common in Mexico; there are single records from Colombia and Haiti.

7. **Taraxacum calocephaloides** A. J. Richards, sp. nov Holotype: Mexico: Distrito Federal: Del Coyoacan Pedregal de San Angel, *A. Sharp and C. L. Gilly* 11 (MICH).

Planta mediocris ad grandis. *Folia* erecta, 100-300 mn longa, prasino-viridia, lobata. Lobi laterales (2)-3-(4) patentes vel subrecurvati, integri vel dentati, deltoidei Lobus terminalis brevis, obtusus vel subrotundatus, in terdum apiculatus. *Petiolus* exalatus viridis vel roseo purpureus ad basin. *Scapi* folia excedentes, glabri ve araneoso-pilosi sub involucro. *Squamae exteriores* multae parvae, recurvatae, 4 × 1.4 mm, olivaceo-virides vel ruf escentes, albo-marginatae, ecorniculatae. *Capitulum* 25-3 mm diametro, citrinum; ligulae stria brunneo-purpure extus notae; stylus stigmaque obscuro-viride, pollin ferum (interdum parce). *Achenium* stramineum 3.0 mn longum (pyramide exclusa), apice patenter spinulosum ceterum rugosum, in pyramidem cylindricam 0.8 mn abrupte abiens. *Rostrum* 7 mm longum, tenue. *Pappu* subalbus. E sectione *Mexicana.*

REPRESENTATIVE SPECIMENS: **Mexico:** DISTRITO FEDERAL: Sierra d Guadalupe, Chiquihuite y Ticoman, *M. Bopp* O. 316 (MEXU); Cu huacan. 21.5.1913. *F. Salazar* (US); Edo. Texcoco, Ahuehuet 2250 m, *E. Matuda* 25861 (US); Luebla Rancha Losada, 2194 m *J. Nicolas* 65 (US). PUEBLA: Arzobispado, 2165 m, *G. Arsène* 197 (US); Santa Rita Ranch, 1500 m, *R. Runyon* 874 (US). VERA CRUZ Boca del Monte, *E. W. Nelson* 226 (US).

Taraxacum calocephaloides is a tall species with pal involucres and white-margined exterior bracts. Th achenes are large for the section, with a long cylindrica cone, recalling those of *Erythrosperma* or *Erythrocarp* species, and the leaf-shape strongly resembles that of *T calocephalum* H. M. em. Dahlst., in the latter section. Th characteristic involucre bears no resemblance to those o these taxa however. It is apparently restricted to moder ate and high altitudes in Mexico.

8. **Taraxacum cuzcense** A. J. Richards, sp. nov. Holotype: Chile: Puenta Alto, near Santiago, 3.10.1919, *E. W. D. and M. M. Holway* (US).

Planta mediocris usque subhumilis. *Folia* erecta (usque ascendentia), 50-100 mm longa, prasino-viridia, anguste subspathulata, lobata. Lobi laterales 2-3, breves, recurvati, anguste triangulares usque subdeltoidei, acuti, in apicem attenuatum abientes; interlobi curvati integri; lobus terminalis subacutus vel obtusus integer; petiolus brevis roseus exalatus. *Scapi* erecti, folia aequantes, araneoso-pilosi. *Squamae exteriores* recurvatae, 5 × 1.5 mm, pallidae pagina superiore, nigrescentes pagina inferiore, emarginatae, ecorniculatae. *Capitulum* 15-20 mm diametro, citrinum; ligulae extus stria cano-violacea notatae; stylus stigmaque obscurum, polliniferum. *Achenium* stramineum, 2.5 mm longum (pyramide excluso), apice erecto-spinulosum, ceterum laeve, in pyramidem conico-cylindricam 0.5 mm subabrupte abiens. *Rostrum* tenue, 5 mm longum. *Pappus* albus. E sectione *Mexicana.*

REPRESENTATIVE SPECIMENS: **Peru:** CUZCO: 3500-3700 m, 3.1925, *F. L. Herrera* (US); 3500-3700 mm, *V. N. Rose* 19038 (US); 11,000 ft, 10.1933, *D. Stafford* (K); AREQUIPA: Pichu Pichu, 13,500 ft, *D. Stafford* 696 (K).

This species is best known by its numerous, small, blackish involucres, and narrow, rose-coloured petioles. It seems to be a species of high altitude in the Andean Chain, from which it is at present only known from two widely separated areas.

9. **Taraxacum craspedotoides** A. J. Richards, sp. nov. Holotype: Venezuela: Huacha, La Venta-Laguna, 3450-3650 m, *Harriet G. Barclay and Pedro Juajibioy* 9862 (US).

Planta mediocris, subtenella. *Folia* olivaceo-viridia, ascendentia, 80-150 mm longa, lobata, anguste lanceolata. Lobi laterales 2-3, breves, recurvati, integri vel paulo

dentati, margine superiore sat convexi; lobus terminalis brevis, subacutus, integer; petiolus longus (ad dimidum longitudinis folii toti), angustus, exalatus, roseus. *Scapi* folia aequantes, araneosi, deinde glabrescentes. *Squamae exteriores* patentes, 5 × 1.5 mm, emarginatae, vel leviter pallide marginatae, ecorniculatae. *Capitulum* ca. 30 mm diametro, flavum; ligulae stria obscuro-cano-purpurea extus notatae; stylus stigmaque sordide viride, parce polliniferum. *Achenium* ignotum. E sectione *Mexicana.*

REPRESENTATIVE SPECIMENS: **Venezuela:** MERIDA: Paramo de la Sal, 3400 m, *A. Jahn* 518 (US); Timotes-Pico del Aquila, 3000 m, *L. Aristeguiela* 2126 (NY); Paramo de Mucuchies, 3000 m, *A. Jahn* 803 (US); Sierra Nevada de Merida, 10,000′, *E. P. de Bellard* 221 (US).

Taraxacum craspedotoides is best known by its narrow leaves with short recurved lobes with convex distal margins. The involucre resembles that of *T. argutifrons.* The plant bears a strong superficial resemblance to *T. craspedotum* Dahlst. (section *Spectabilia* Dahlst.). However, the involucre is quite different, being quite characteristic for the section *Mexicana.* It is known only from high altitude in a restricted area of Venezuela.

10. **Taraxacum disseminatoides** A. J. Richards, sp. nov. Holotype: Mexico: Distrito Federal: Canada de Contreras, *H. Farias* R38 (MEXU).

Planta mediocris, tenella. *Folia* laete viridia, erecta, c 100 m longa, lobata, spathulata. Lobi laterales 2-3, triangulares, dentati, acuti; lobus terminalis deltoideus, obtusus, vel tripartitus et apiculatus; petiolus angustus, exalatus, roseus. *Scapus* singularis vel scapi pauci, araneoso-pilosi, folia excedentes. *Squamae exteriores* erectae, 4 × 1 mm, pallide olivaceo-virides, submembranaceae, pallide marginatae, ecorniculatae. *Capitulum* 15-20 mm diametro, citrinum; ligulae extus stria canopurpurea notatae; stylus stigmaque sordide viride, epolliniferum. *Achenium* brunneo-stramineum, 2.8 mm (pyramide exclusa)

tuberculatum ad apicem, ceterum laeve, in pyramidem cylindrico-conicam 0.5 mm subabrupte abiens. *Rostrum* 5 mm. *Pappus* sordide albus. E sectione *Mexicana.*

REPRESENTATIVE SPECIMENS: **Mexico:** DISTRITO FEDERAL: Tlalpam, Valley of Mexico, 16.8.1902, *C. G. Pringle s.n.* (US).

Taraxacum disseminatoides has leaves of a characteristic pale green. The large dentate, strictly triangular, somewhat distant leaf-lobes are distinctive, and reminiscent of some forms of the *Erythrosperma*-species *T. disseminatum* Hagl. The involucre, with very small, erect, submembranaceous, pale olive bracts, is highly characteristic. The achenes recall those of *T. argutifrons.* It is recorded from two stations in Mexico.

11. **Taraxacum tenejapense** A. J. Richards, sp. nov. Holotype: Mexico: Distrito Federal: Nevada de Toluca, Ojas de Agua, 12,800 ft., 1.4.1938, *E. K. Balls* (K).

Planta mediocris. *Folia* olivaceo-viridia, ascendentia, 80-150 mm, lanceolata, lobata. Lobi laterales 2-4, recurvati, subhamati, margine superiore sat convexi, integri vel 1-dentati (interdum multi-dentati margine inferiore); lobus terminalis subacutus vel rotundatus mucronatus, subhamatus, integer; petiolus nervusque medianus pallide virides, petiolo brevi angusto exalato. *Scapi* folia subaequantes per anthesin, deinde elongati, subtenues glabrescentes vel sparsim pilosi cupreo-virides. Squamae exteriores recurvatae, pallide virides, tenues vel sat membranaceae, 8-10 × 1-2 mm, vix marginatae, ecorniculatae; squamae interiores obscuriores. *Capitulum* 35-40 mm diametro, pallide flavum; ligulae stria obscura colore incerto extus notatae; stylus stigmaque siccum obscurum vel subnigrum polliniferum. *Achenium* stramineo-brunneum vel pallide brunneum, 3.5 mm, tuberculatum et spinulosum ad apicem, in pyramide cylindra 0.7 mm abrupte abiens. *Rostrum* 10-13 mm. *Pappus* sordide albus. E sectione *Mexicana.*

REPRESENTATIVE SPECIMENS: **Mexico:** CHIAPAS: Tenejapa, steep slope with *Quercus* and *Magnolia* in the Paraje Matsab, 8900′,

Alush Shilom Ton 675 (IPN); Tenejapa, slope with *Quercus* and *Liquidambar* at Paraje Shohle, 8200′, *Alush Shilom Ton* 765 (IPN, NY); San Cristobal Las Casas, cornfield, 6900′, *D. Breedlove* 6775 (MICH); Seltepec, Ventana, 2100 m, *E. Matuda* 4544 (NY). MEXICO: Valley of Mexico, *E. Matuda* 2231 (MICH). **Guatemala:** Chimaltenango, Santa Elena, 2400-2700 m, *A. F. Skutch* 104 (MICH). **Costa Rica:** Cartago, Volcán Irazu, 3200 m, *R. J. Taylor* 4434 (NY).

Taraxacum tenejapense has a leaf form between *T. mexicanum* and *T. unguilobifrons* or *T. craspedotoides*, with rather short, scarcely dentate, recurved subhamate leaf-lobes. However, it is readily known from these and all other species in section *Mexicana* by the long achenes and exterior bracts. The form of the achenes, with the rather short, cylindrical cone; the discoloured pappus; and the thin, almost membranous exterior bracts, which contrast palely with the darker interior bracts, are all characteristic of this section.

This seems to be a species of moderate altitude in south Central America.

Section Arctica Dahlst., Acta Fl. Sueciae, 1:37 (1921) emend. Richards, Bot. J. Linn. Soc. 65:39 (1972).

This is the only bipolar section of *Taraxacum*. It occurs circumboreally at very high latitudes, and in various mountain systems of the Northern Hemisphere, including the North American Rockies, where *T. rupestre* Greene and *T. scopulorum* A. Gray reach south to Colorado, Idaho and Montana (two little known Californian species, *T. ammophilum* Nels., and *T. californicum* Mz. and Ttn. may also belong to this section). Four species are known from South America, mostly around the southern tip, although *T. andinum* extends to Aconcaqua, Argentina (near Santiago, Chile). There is thus a gap of some 8000 km between the North and South American stations. *T. magellanicum*, which is the most widespread of the species in Tierra del Fuego, is also common in New Zealand and has been recorded from Chatham Island. Two related species (*T. cygnorum* H. M. and *T. aristum* Hagl. and Markl.) are found

in Australia, completing the picture for a remarkably widespread, disjunct, and presumably ancient section (Richards, 1973). The South American species are as follows (all known stations are given):

12. **Taraxacum magellanicum** Commers. ex C. H. Schultz-Bipont, Flora: p. 122 (1855); Dahlstedt H., Ark. Bot., 6(12): 5 (1907) (fig.).

T. ibari Philippi, Anal. Univ. Chile, 87:324 (1894).

T. melanocarpum H. M., Monogr. Gatt. Taraxacum: 54 (1907).

Type locality: **Chile.** Magellan, Purta Arenas. 1852. *W. Leckler* pl. magellanicae 1103 (S).

ADDITIONAL LOCALITIES ARE: **Argentina:** TIERRA DEL FUEGO: Estancia Harberton, Campo Afuera, 54°48′S, 67°27′W, 450 m, *D. M. Moore* 1390 (K); Campo Rancho Tombo, 54°52′S, 67°16′W, *D. M. Moore* 1367 (K); Estancia Moat, Rio Chico, 54°53′S, 66°53′W, 700 m, *D. M. Moore* 1634 (K); Isla Navarvno, *C. Skottsberg* (US); Orange Harbour, 1919, *Capt. Wilkes* (US); Rio Garde, *T. Mexia* 7929 (K, US); Rioblanco Cordillera de los Bagnales, 5.1879. *H. Ibar* (K) (type of *T. ibari*); Sierra Almanza, Gerro Almanza, 54°50′S, 67°29′W, 900-1100 m, *D. M. Moore* 1419 (K). **St. Cruz:** 12.11.1928, *A. Donat* (K) (as *melanocarpum*); Estancia Las Vegas, Los Vascos, 51°19′S, 70°20′W, *D. M. Moore* 1315 (K); Guar Aiken, road, 25 km south Puerto Oyle, 2.1.1939, *W. J. Ryerdam et al.* (K); Lago Argentina, Brazo Rico, 17.12.1950, *H. Sleumer* (US); Estancia Fitzroy, Rio de las Vueltos, 450 m, *H. Sleumer* 1265 (US). **Chile:** Cordilieres de Neaute, 1855, *P. Germain* (K) (type of *T. melanocarpum*); Magellan, Loredo Bay, 22.1.1888 *L. A. Lee* (US); Gregory Bay, 18.1.1888, *L. A. Lee* (US); 23.11.1886, *W. E. Safford* (US); Puerto Williams, Navarino Islands, 7.1.1959, *E. J. Godley* (K).

Taraxacum magellanicum shares with other South American members of sect. *Arctica* a fusiform achene with scarcely differentiated cone, a short (to 6 mm) rostrum to the achene, a white pappus, short, wide erect exterior bracts, and smooth, rather small leaves. It is distinguished from other members of the group by wide scarious margins to the bracts, and narrow, scarcely lobate leaves. It

is remarkably variable, and may usually be sexual: a chromosome count of $2n = 16$ (diploid) has been recorded by D. M. Moore (pers. comm.).

13. **Taraxacum andinum** Dahlstedt, Ark. Bot., 6(12):13 (1907) (fig.).

Type locality: **Argentina:** Las Cuevas, Horcon, Aconcagua, 3000-3100 m, *G. O. Malme* 2865 (S).

ADDITIONAL LOCALITIES ARE: **Argentina:** Terra del Chubut, Valle de la Laguna Blanca, 45°52′S, 71°15′W, 15.11.1902, *J. Koslowsky* (K). **St. Cruz:** Estancia Guer Aike, *H. Steumer* 877 (US); Puerto San Julian, 1.12.1927, *M. E. Blake* (K); Rio de las Vueltas, *H. Steumer* 1362 (US); Rio Gallegos, *H. Steumer* 779 (US). **Chile:** Magellan, 78 km north-west of Punta Arenas, *W. J. Eyerdam et al.* 24145 (K).

Taraxacum andinum is characteristically a more dwarf and stockier plant than *T. magellanicum,* with a broader and much more dissected leaf. It also differs in the exterior bracts, which usually exceed 3 mm in width, and have narrow white or rose margins. It is dubiously distinct from *T. gillesii* (see below).

14. **Taraxacum gillesii** W. J. Hooker and G. A. W. Arnott in Hooker, Companion Bot. Mag., 1:31 (1835).

Type locality: **Chile.** Las Guindas, Andes of Mendoza. *Dr. Gilles* (? date) (K).

ADDITIONAL LOCALITIES ARE: **Argentina:** TIERRA DEL FUEGO: Cabo San Vincente, 23.11.1969, *R. N. P. Goodall* (RU); Estancia moat, Rio Chico, 54°53′S, 66°53′W, 700′, *D. M. Moore* 1634 (RU).

This species is dubiously distinct from *Taraxacum andinum,* but has even shorter, wider and more dissected leaves, scapes shorter than the leaves, and concolorous bracts; it may prove to be an extreme form of *T. andinum,* but at present I am continuing to regard it as a separate species.

15. **Taraxacum rhusiocarpum** Dahlstedt, Ark. Bot., 6(12): 15 (1907) (fig.).

Type locality: **Argentina:** PATAGONIA: Between Kark and Eberhardt, in woods, 31.3.1899, *O. Borge* 354 (S).

This species has never been recollected, but it seems to be distinctive: the narrowly lobed leaves approach some forms of *Taraxacum magellanicum,* but it has rather broad, narrowly margined exterior bracts (similar to *T. andinum*), chestnut or reddish achenes, and lacks pollen. It requires rediscovery.

Section Vulgaria Dahlst., Acta Fl. Suec., 1:37 (1921).

This section is apparently restricted in the native state to Europe; two species in Asia may be introductions which have not yet been found in their native localities. They are common and invasive weeds of open ground, grasslands, etc. and have become adventive in many parts of the world, including North America, South Africa, Australia, New Zealand and South-East Asia. Although they have been recorded in South and Central America under the aggregate species name *Taraxacum officinale* Weber, there exist no records of the individual microspecies (the section is almost entirely agamospermous and contains some 400 agamospecies). The species in this section are frequently very plastic, and in Europe are difficult to identify outside the main flowering season. Perhaps because of different day-lengths, etc., members of this section from the Southern Hemisphere tend to be particularly difficult to identify with certainty, and the majority of identifications listed here are tentative, the material being atypical. Species in sect. *Vulgaria* occurring in neotropical regions will be known by their robust stature and long exterior bracts (exceeding 8 mm). The achenes lack a distinctive cone, the rostrum exceeds 8 mm, and the pappus is white.

16. **Taraxacum bracteatum** Dahlst., Ark. Bot., **19**(18):11 (1925).

Mexico: Erongaricuro, seed collected 30.4.1968, *Lindenbergh.* Cultivated *van Soest* (L).

17. **Taraxacum angustisquameum** Dahlst. ex H. Lindberg f., Medd. Soc. F. Fl. Fenn., **35:** 13. (1908).

Chile: Cerra San Christobel, 800 m, 2.4.1967, *J. L. van Soest* (L); El Golf, 1.5.1967, *J. L. van Soest* (L); Santiago, Park by Mapocho River, 6.4.1967, *J. L. van Soest* (L).

18. **Taraxacum copidophyllum** Dahlst., Ark. Bot., **9**(10):25 (1910).

Chile: Santiago, 21.4.1967, *J. L. van Soest* (L).

19. **Taraxacum cordatum** Palmgr., Acta Soc. F. Fl. Fenn., 34(1):12 (1910).

Colombia: CUNDINAMARCA: Macizode Bogota, Quebrada del Rosal, 3000 m, 29.6.1939, *J. Cuatrecasas* (US). **Guatemala:** Quezaltenango, Volcan St. Maria, 3770 m, *J. H. Beaman* 4101 (US).

20. **Taraxacum marklundii** Palmgr., Acta Soc. F. Fl. Fenn., 34(1):20 (1910).

Chile: Santiago, 21.4.1967, *J. L. van Soest* (L).

21. **Taraxacum raunkiaerii** Wiinst., Dansk Ekskurs. Fl., 5th Ed., 303 (1934).

Argentina: TIERRA DEL FUEGO: Varela Peninsula, Estancia Harberton, 2.11.1968, *N. P. Goodall* 1835 (MICH).

22. **Taraxacum vastisectum** Makl., Act. Bot. Fenn., **23:** 120 (1938).

Chile: Santiago, 21.4.1967, *J. L. van Soest* (L).

Section Erythrosperma (H. Lindberg f.) Dahlstedt,

Act. Fl. Suec., **1**:41 (1921)

emend. H. Lindb. f., Acta Bot. Fenn., **17**:8 (1935).

The *Erythrosperma* are small delicate plants, native to dry areas of Europe and western Asia; there are about 130 agamospecies, a number of which have been found adventive in other areas, including North America (van Soest, 1958). They are diagnosed by fruits bearing long (ca. 1 mm) cylindrical cones (similar to sect. *Mexicana*), but which are more usually reddish or purple in hue, and short exterior bracts which are most commonly corniculate (i.e., with an appendage just below the apex).

Erythrosperma species cannot be confused with section *Arctica*, which have smooth, glabrous leaves, and a fusiform achene without a marked cone, and with a short rostrum; nor with section *Vulgaria* which are grosser plants with long exterior bracts and achenes which lack a markedly cylindrical cone. They do, however, resemble some members of section *Mexicana*, although they are less gross and with more dissected leaves, rarely have membranous or scarious exterior bracts, usually have corniculate exterior bracts and reddish achenes, and always have a white pappus.

23. **Taraxacum fulvum** Raunkiaer, Dansk Ekskurs. Fl., 2nd Ed., 258 (1906).

Haiti: Nord, Marmelade, 800 m, *E. C. Leonard* 8354 (US).

24. **Taraxacum plumbeum** Dahlstedt, Ark. Bot., **10**:6 (1911).

Chile: SANTIAGO: El Golf, 1.4.1967, J. L. van Soest (L).

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REFERENCES

DAHLSTEDT, H. 1907. Ueber einiger Sudamerikanische *Taraxaca*. Ark. Bot. **6**(12): 1-19.

HANDEL-MAZZETTI, H. VON. 1907. Monographie der Gattung Taraxacum. Leipzig und Wien.

RICHARDS, A. J. 1972. The *Taraxacum* flora of the British Isles. Watsonia **9** (suppl.).

————. 1973. The origin of *Taraxacum* agamospecies. Bot. Jour. Linn. Soc. **66**(3): 189-211.

SOEST, J. L. VAN. 1958. *Taraxacum* sect. *Erythrosperma* Dt. em. Lindb. in North America. Act. Bot. Neerl. **7**: 627-628.

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THE FLORA OF PENIKESE ISLAND: THE CENTENNIAL COLLECTION AND ITS BIOGEOGRAPHIC IMPLICATIONS

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The flora of Penikese Island has been studied more extensively than that of any comparable area on the eastern coast of North America. Complete lists of vascular plant species on the island were compiled in 1873 by D. S. Jordan, while an instructor at the Anderson School of Natural History, in 1923 by J. M. Fogg, Jr. (in Lewis, 1924) and in 1947 by E. T. Moul. These latter two collections were made in part by groups commemorating 50th and 75th anniversaries of the Anderson school. Fogg (1930) included Penikese in a larger study of the Elizabeth Islands, listing a number of species not encountered in the 1923 collection. The present study is a flora of the vascular plants occurring on Penikese in 1973 and a comparison of this flora with that in 1873, 1923, and 1947, using recent biogeographic methods, with observations on vegetational changes which have occurred on the island over the last 100 years.

Penikese forms part of the Elizabeth Islands chain and lies at 41°27′ N. latitude, 70°55′ W. longitude, one mile north of Cuttyhunk, the lowermost island of the group, and about 12 miles southwest of Woods Hole, Massachusetts. The island was formed during the last, or Two Creeks, substage of the Wisconsin glaciation, and now consists of two morainal hills joined by a narrow isthmus, totalling about 74 acres in extent with the highest point 86 feet above sea level (Kalisch, 1972). Zinn and Kahn (1972) discuss its geology in some detail. There are no streams and little evidence of dune formation or significant wind erosion, although Penikese is exposed to winds from all directions. The beaches except for a sandy strip on the eastern margin of the isthmus are littered with boulders or rocks of various sizes which impede further erosive actions of wind and water. Eight ponds occur,

one of which, Typha Pond, probably occupies an original kettlehole, the other seven being situated in marked depressions or formed by the coalescing of beaches.

The earliest description of Penikese was written following Gosnold's exploration of the island on May 30, 1602. Gosnold logged cedars, "some of which would make masts for the greatest ships of the world" as well as sassafras (in Gookin and Barbour, 1963). From 1602 to 1873, the island was bought and sold several times, supporting up to three families at any given period. An account of its history is in Howland (1964). In 1873, John Anderson offered Professor Louis Agassiz the island to be used as the site for a school for the instruction of teachers of natural history; construction of the school began that spring. Jordan (1874) described Penikese in 1873 as without trees, nearly without shrubs, scantily covered with pasture grasses, and "about as barren looking a pile of rock and stone as one could well imagine." Of the previous woodlands, only "the rotten roots of a solitary beech stump and a few branches of red cedar and red maple (?) found buried in the muck of a small swamp" remained. The island was heavily grazed by sheep and had been grazed at least since 1797. In addition an estimated 1,000 nesting terns were present (Nisbet, 1973). Jordan collected 108 species of vascular plants from Penikese, all of which were common on the surrounding mainland. Some prominent mainland taxa, including the genera *Aster* and *Solidago*, were then absent from the island.[1]

[1]Jordan also collected on Gull Island, a small island one half mile southeast of Penikese, listing several species including *Lathyrus japonicus*, *Limonium carolinianum*, *Rhus radicans*, and *Solidago sempervirens*, then absent from Penikese. Lewis (1924) described this island, then connected to Penikese at dead low water, in some detail, and Fogg (1930) noted species, including *Rhus radicans* and *Limonium carolinianum*, which had also disappeared from Gull Island. Gull Island was used as a target for bombing practice during the 1947 collecting period and Moul, because of government regulations, was not allowed to visit it. By summer, 1973, Gull Island, devoid of terrestrial vegetation, appeared as a pile of rocks probably under water at high tide.

The Anderson School closed after the summer of 1874 and the island remained uninhabited for about ten years, after which it was resold and used to support a turkey farm and continued grazing by sheep. In 1905, the State of Massachusetts acquired the island to use for isolating smallpox patients and, later, as a leprosarium. Tern populations increased rapidly following protection to an estimated 7,000 birds in 1908. In 1921, the leprosarium was discontinued and the island again abandoned.

In 1923, a plaque commemorating the founding of the Anderson School was fixed to a boulder on the larger of the hills. A biological survey was conducted (Lewis, 1924) during which Fogg listed 166 species of vascular plants present while ecological observations were compiled by Margaret Shaw. The island had been uninhabited for two years; sheep had been removed and grasses were abundant. *Ammophila breviligulata* covered the slopes of the west shore; areas in the northern grasslands were denuded by terns (*Sterna hirundo* and *S. Dougallii*) which nested there in June. Some woody species, including *Rhus typhina, Sambucus canadensis, Myrica pensylvanica,* and one specimen of *Quercus rubra* had invaded. Species of *Aster* and *Solidago* were well established in the grasslands. The increase (58) in total species since 1873 may be explained in part by changes in land use, including the abolition of grazing, the accidental introduction of weed species, and the deliberate introduction of persistent ornamentals and vegetables.

During summer, 1923, most of the ponds showed marked zonation with floating algae surrounded by a zone of sedges (including *Eleocharis obtusa, E. palustris, Scirpus americanus,* and *S. paludosus*), a band of *Spartina patens,* and an irregular band of *Iris versicolor* adjacent to the grasslands. Typha Pond was surrounded by concentric zones of *Typha latifolia, Juncus acuminatus,* and, adjacent to the grasslands, *Scirpus paludosus. Salix alba* × *fragilis* occurred at both ends of the pond. On the northwestern portion of the larger section of the island, the ponds were

more shallow and surrounded by large stands of *Bidens connata*. Dry Pond had apparently contained water in the spring but was dry in August and lacked vascular plant species; Tern Pond was surrounded by a zone of *Spartina alterniflora* and *Dryopteris thelypteris*.

During the period 1924 to 1930, Fogg made additional trips to Penikese, collecting more than 20 previously unreported species. In 1925, much of the leprosarium was demolished and the island was transferred to the Massachusetts Division of Fisheries and Game for use as a bird sanctuary. Various game species were introduced along with a variety of plants intended as food for wildlife. The breeding population of terns increased through 1932, suffering an abrupt decline that year for reasons which are largely unexplained (Floyd, 1932). In 1933, breeding herring gulls (*Larus argentatus*) were first observed on Penikese (Floyd, 1933). From 1925 through 1939, one or more caretakers were resident on the island; from 1939 through 1973, no-one has resided there year-round.

During summer, 1947, E. T. Moul collected 158 species of vascular plants on Penikese. He noted little change in the vegetation since 1923. Dominant species of the tension line and grassland communities were the same; many of the escaped cultivated species had not persisted, however, perhaps because of the several hurricanes which had drenched the island with salt spray. *Rhus radicans*, previously absent, occurred in stunted form in the high grasslands. Thickets of *Sambucus canadensis* had increased in size and number, particularly along stone walls and in depressions. Seven clumps of *Morus alba*, previously unreported, were well established on the hill behind Tub Pond. Trees and shrubs in more exposed habitats did not appear to have increased in size or number. Terns were variously estimated at 2,500 and 10,000 birds (Nisbet, 1973) and nested over much of the island. Herring gulls were estimated at 2,000 birds (Zinn and Rankin, 1952).

The vegetation around the ponds was similar to that in 1923 as well. Typha Pond had the richest, most diversified

flora; the willows previously found nearby had been, however, cut. Dry Pond was unchanged, though some water may have been present earlier in the year. Leper and Tern Ponds were dry in early July; these were no longer surrounded by *Bidens connata*, but supported large stands of *Polygonum punctatum* and *Rumex maritimus*. South and Tub Ponds were brackish with characteristic halophiles surrounding them. The marsh on the east shore had a flora similar to that of Typha Pond, a change from its previous brackish condition.

Moul made one trip to Penikese in 1961. *Daucus carota*, *Datura stramonium*, and *Chrysanthemum leucanthemum*, previously very common, were then rare. The island apparently had been overrun by gulls in the late 1950's (Nisbet, 1973); breeding terns were absent. A number of shrubs, including *Rhus copallina*, *Rubus laciniatus*, and *Sambucus canadensis*, had spread. *Pinus sylvestris* had become extinct, while specimens of *Acer pseudoplatanus*, thickets of *Populus alba*, none more than five feet tall, and a single specimen of *Populus deltoides*, badly salt-spray-damaged, remained. Two ferns, *Dennstaedtia punctilobula* and *Dryopteris thelypteris* were absent from their former sites, while *Raphanus raphanistrum*, previously restricted, was established in large pure stands (Moul, 1961).

By summer, 1973, Penikese had lacked a resident human population for 44 years. A large breeding colony of herring gulls and black-backed gulls (*Larus marinus*) was present; no nesting terns were seen. On the north side of the island, an old stone dock, presumably built prior to the founding of the Anderson School, remains in fairly good condition. Behind the dock are a series of foundations and stone walls. Near the summit of the hill on which the commemoration plaque for the Anderson School is fixed is a small reservoir, still holding water, and the foundation of a smaller similar structure. On the west side of the larger portion of the island, foundations of the leper cottages are still visible. One small cement building stands at the northeast end of the row of cottages; eastward

behind the cottages is a small cemetery. There are no signs of previous human habitation on the smaller portion of the island.

In June, all of the ponds except Dry Pond held water; by July 14, water level had fallen markedly. On August 8, Rankin Pond, formed within the last 26 years to the northeast of Tern Pond, was completely dry and Leper Pond was nearly so. Water level in the marsh had dropped considerably.

By August 8, most of the gulls had left the island. There were two campsites present at this time, one of the occupants claiming to have camped on Penikese for six weeks each summer for the last ten years. Earlier in 1973, the island was subcontracted to the State Department of Youth Services to be used in part for a school for problem youths. By September the building of this facility had begun and a temporary campsite was constructed. A small tractor hauled equipment from the dock up to the site of the school, enlarging what had been for at least 100 years a footpath.

For the purposes of this study, seven trips were made to Penikese in summer, 1973, on the following dates: June 12, July 14 and 15, August 8, 9 and 13, and September 20. Specimens of 163 vascular plant species were collected in identifiable condition. The grasslands, quite thick over most of the island, contain denuded areas and numerous paths made by the gulls. *Rumex acetosella* frequently dominates gull nesting sites. Dominant grasses are *Ammophila breviligulata* on the southeast side, *Agrostis stolonifera* in clumps around the ponds, *Holcus lanatus* on the west side of the island, and *Agrostis tenuis, Anthoxanthum odoratum* and *Poa pratensis* throughout. Thick patches of *Solidago sempervirens, S. rugosa,* and *S. tenuifolia* are scattered across the larger hill. *Chrysanthemum leucanthemum* is again abundant, particularly on the smaller section with *Achillea millefolium; Daucus carota* remains, as in 1961, extremely scarce. A single specimen of *Dennstaedtia punctilobula* was noted; *Datura stramonium* is again common, particularly in the tension line.

Over the last 26 years, there has been a marked increase of shrubs and woody vines. *Rhus radicans* occurs in dense patches in the upper grasslands on the main portion of the island, and *R. copallina* is well established in grasslands behind the wharf, with a small stand on the western side. *Rosa rugosa*, reported previously only on the east side of the main portion of the island near the dock, is now well established over the main portion and borders South, Typha, and Leper Ponds and the marsh. A thick patch occurs near the wharf. *Rhus typhina* and *Myrica pensylvanica,* found in 1923 and 1947 in only one location each, are well distributed over the larger hill.

Penikese has no clearly defined zones resulting from the effects of wind-borne salt spray, as do other nearby coastal areas (Boyce, 1954). The "tension line" is that portion of land between the beach and areas supporting grasslands and on Penikese is underlain largely by eroded glacial deposits. Plants common to this zone in 1973 include *Rumex crispus, Phytolacca americana, Mollugo verticillata, Glaucium flavum, Lepidium virginicum, Raphanus raphanistrum, Lathyrus japonicus, Anagallis arvensis, Lycopersicum esculentum, Solanum dulcamara, S. nigrum, Verbascum thapsus, Matricaria matricarioides,* and *Sonchus asper.* Halophytes, including the widespread and often frequent *Cakile edentula,* are rare.

Typha Pond no longer contains *Typha latifolia,* which now occurs only in one small stand within the marsh, the salinity of which has dropped off steadily since 1947 (Zinn and Rankin, 1947; Rich, 1973). Typha Pond has not become more saline than in previous years and the extinction of *T. latifolia* there cannot be easily explained. The pond is surrounded by *Agrostis stolonifera, Panicum virgatum, Rosa rugosa,* scattered *Polygonum punctatum,* and *Aster novi-belgii.*

The change from salt to fresh water in the marsh may have caused the loss of salt marsh species noted in previous collections. Jordan collected *Iva frutescens, Salicornia europaea, Suaeda maritima, Spartina patens,* and *S. alterni-*

flora there. Fogg and Moul collected only the two Spartinas. In 1973, *Polygonum punctatum* and *Pluchea purpurascens* are abundant on the edges of the marsh; *Iris versicolor* is common on the northern end with a clump of *Rosa rugosa*. *Solidago sempervirens* and *Sambucus canadensis* grow among thick clumps of *Agrostis stolonifera*; *Juncus gerardi* is scattered at intervals along the edge.

Dry Pond supports large stands of various grasses, *Polygonum persicaria*, *Rubus frondosus*, *Sambucus canadensis* and *Solidago rugosa*. There was no evidence that the pond held water earlier in the spring. The zonation surrounding other freshwater ponds in 1923 and 1947 is no longer present. Many freshwater marsh plants, including *Eleocharis palustris*, *Scirpus americanus*, *S. paludosus*, and *S. validus*, apparently became extinct sometime after 1947. The presence of numerous herring gulls resting within these ponds may have contributed to the elimination of these species.

Tern Pond is surrounded by grasses with scattered *Iris versicolor*, *Polygonum persicaria*, *P. punctatum*, *Phytolacca americana*, *Solidago rugosa*, and *S. sempervirens*. *Ludwigia palustris*, *Myriophyllum verticillatum*, and *M. pinnatum* were collected in dried mud and in shallow water on its bottom.

Leper Pond is surrounded on the east and southeast sides by *Agrostis stolonifera*, *Phytolacca americana*, and *Solidago sempervirens* and by *Rhus typhina* and a small grove of *Salix alba* × *fragilis* on the west and southwest. *Ludwigia palustris* is abundant on the bottom. Only low grasses border the northeast, most-exposed end.

South Pond, the largest pond on the island, with Tub Pond is most exposed to wind-borne salt spray. *Iris versicolor* and *Rosa rugosa* are scattered along the northwestern edge; *I. versicolor* and *Panicum virgatum* dominate the northeastern border. The southern end is rocky with interspersed tension line species.

Tub Pond, located on the smaller section of the island, is separated from the ocean on the east, west, and south

sides by only a short rocky beach. A cliff to the north is covered chiefly by *Agrostis tenuis, Panicum virgatum, Achillea millefolium,* and *Solidago sempervirens.* Tension line plants, including *Phytolacca americana, Anagallis arvensis,* and *Solanum dulcamara,* are dispersed among the rocks along its edge. The salinity of the pond increased from 9 o/oo to 34.4 o/oo during the period 1923 to 1947 (Zinn and Rankin, 1952); the pond lacked submerged macrophytes in 1973.

Rankin Pond is surrounded by grasses, *Polygonum persicaria,* and *Solidago sempervirens.*

Several plants new to Penikese in this collection were quite abundant during summer, 1973. *Glaucium flavum* is the dominant species, represented by hundreds of individual plants, on the rocky isthmus between the two portions of the island and is also found in the tension line on the south side of the island below South Pond. Seymour (1969) reports this species as rare on shores in Bristol County and on Naushon Island, Massachusetts, while Hehre and Conway (1969) reported three colonies, totalling 20 plants in all, in West Falmouth, Mass. *Matricaria matricarioides* is abundant on the tension line on the southwest side of the larger section of the island, below the old leper cottages, and in the tension line on the southwest side of the smaller portion of the island. New escapees from cultivation, aside from the tomato, are muskmelon, *Cucurbita melo,* in a depression near Tub Pond and English ivy, *Hedera helix,* the flowering form of which was found near the old leper colony foundations on the southwest shore.

BIOGEOGRAPHIC CONSIDERATIONS

Two themes have recurred in discussions of the flora and vegetation of Penikese and other islands, the problem of successional development of the vegetation and the interpretations of differences between successive plant lists. Jordan (1874) felt that his list might be of general

interest "as showing which plants survive a prolonged struggle against grass and sheep." Shaw (in Lewis, 1924) suggested that on Penikese, forest might "again develop provided the land is neither pastured or cultivated." Lewis, in the same paper, noted that "ecologically the island is progressing rapidly" in the 12 years without sheep and postulated that man was the most efficient agent for the introduction of new species. Fogg (1930), in a detailed analysis of invasions since 1873, by his reckoning about 20 garden escapes, an equal number of cosmopolitan adventives, and over 50 native species, raised the difficulty of understanding why so many invaders since 1873 "should have been kept down until recent times when so many others were not only present in 1873 but have survived . . ."

Moul (1948), noting that the general aspect of the vegetation had not changed for 24 years, suggested that the flora consisted of two groups of species, one adapted to the ecological conditions of the island, the other consisting of colonists which were periodically wiped out. In 1961, noting the decrease in tree populations and the extinction of *Pinus sylvestris* on Penikese since 1947, he concluded that "the evidence indicates a grass 'subclimax' may persist indefinitely."

An interesting dimension to the problem of island diversity was added by Preston (1962) and MacArthur and Wilson (1963) who suggested that on oceanic islands a balance of immigration by extinction might exist so that the diversity of at least some biotas might be understood as an equilibrium. This theory, developed more fully in MacArthur and Wilson (1967), postulates that during early successional stages the rate of extinction will tend to decrease in areas of sufficiently varied topography, permitting an increase in the total flora. Penikese is, of course, a land bridge or continental island, separated from the mainland during the last rise in sea level. MacArthur (1972) suggests that small land bridge islands experience initially high extinction rates when separated from the mainland and rapidly reach equilibrium in the manner of

Table 1. Total flora at each collection period, invasions, re-invasions, extinctions, and persisting species.

Collections	Number of species
1873	108
1923	166
persistent since 1873	70
extinctions since 1873	38
invasions since 1873	96
1947	158
persistent since 1873	55
persistent since 1923	59
extinctions since 1923	52
invasions	
invasions since 1923	35
re-invasions from 1873 flora	9
1973	163
persistent since 1873	47
persistent since 1923	45
persistent since 1947	18
extinctions since 1947	48
invasions	
invasions since 1947	34
re-invasions from 1873 flora (went extinct by 1923)	5
re-invasions from 1923 flora (went extinct by 1947)	14

oceanic islands. The history of the flora of Penikese appears to be a striking corroboration of the equilibrium concept. Table 1 contains the total number of vascular plant species present at each collection period, as well as invasions, re-invasions, extinctions, and persisting species. The total number of species in the floras in 1923, 1947, and 1973 varies within a range of only eight species. The

marked increase after 1873 can easily be explained by changes in land use, particularly the elimination of grazing sheep, which permitted some successional development within that period. Extinctions from each flora apparently occur abruptly and then less drastically in successive collections, supporting Moul's separation of the flora into permanent and temporary elements. Species lost from the 1873 flora were 38 by 1923, 15 between 1923 and 1947, and 8 between 1947 and 1973, excluding re-invasions in the latter instances. Similarly the loss from the 1923 flora was 52 during the period 1923-47 and 22 between 1947 and 1973.

Table 2. The Simpson Index of Resemblance comparing all collections at the specific level.

Time Interval (years)	Collections compared	Resemblance
100	1873-1973	60.2
74	1873-1947	59.2
50	1873-1923	64.4
50	1923-1973	65.0
24	1923-1947	72.0
26	1947-1973	71.0

We have used the Simpson index of resemblance (Simpson, 1965) to compare the taxonomic composition of the floras at each collection period. This index ($100c/_{n1}$ in which c is the number of taxonomic units common to the two floras and n_1 the total number of units in the smaller of the two) seems particularly useful in comparing floras of approximately equal numbers occurring in a single area. Changes in the floristic composition of successive floras seem to have occurred in a quite even manner (Table 2). Although, as would be expected, floras most distant in time are most dissimilar, the resemblances throughout the 50 year intervals 1873-1923, 1923-1973 or the shorter periods 1923-1947, 1947-1973 are remarkably alike.

We have also compared the ratios of non-native to native species in the various floras (Table 3); these ratios have declined since the 1873 collection, when non-natives outnumbered native species, increasing slightly between 1947 and 1973. They have remained throughout the period strikingly higher than those of adjacent coastal areas (Burk, 1968). The overall decline in non-natives since 1873 may be attributed to decreasing disturbance on the island as well as to the larger pool of native species available for colonization in surrounding areas. The latter increase may well be attributed to the action of the herring gulls, which forage in mainland dumpsites where non-native species are abundant, as agents of dispersal.

Table 3. Number of native and non-native species in successive floras and the ratio non-native/native species.

Collection	Native species	Non-native species	Ratio non-native/native
1873	53	55	1.04
1923	87	79	.91
1947	91	67	.74
1973	87	76	.87

Pike and Hodgdon (1962), evaluating changes in the flora of Machias Seal Island over an 18 year period, raise the problem of what constitutes a definitive flora in areas where striking changes in floristic composition occur rapidly. Island biotas are increasingly interesting for practical as well as theoretical reasons (Kolata, 1974; Willis, 1974); we suggest that for maximum utility, two different kinds of island floras must be maintained, compendia of all species ever collected (on Penikese this would number over 280) and a series of lists of species present during clearly delimited, relatively short intervals of time.

A reconnaissance of Penikese on July 9, 1974, suggests further explanations of recent changes in the vegetation

and hints at what may be anticipated there. The drought of the early 1960's may have contributed to the elimination of zonation in the ponds. The 1974 season to date had been much drier than 1973, and Typha Pond was lower than at any time the previous season. *Scirpus americanus*, not seen in several careful surveys of the pond during 1973, was fairly abundant on the muddy stratum below what had been low water mark that year. These plants were severely cropped by gulls; in addition clumps of grasses at the edges of the pond showed the effects of heavy grazing by muskrats. All ponds on the west side of the island were already dry, including Tern Pond, which held water through the year before; the pond bottoms were already invaded by a variety of herbs including *Polygonum* spp. *Rumex crispus*, *Ludwigia palustris*, *Anagalis arvensis*, *Gnaphalium uliginosum*, and *Pluchea purpurascens*. Vegetation generally throughout the island was less lush than in 1973. In addition, since the previous autumn several buildings had been constructed on the east side near the dock; a large vegetable garden had been laid out, and the reservoirs were being cleaned and repaired. The period of no year-round human activity on the island has clearly ended and new patterns of disruption, with concomitant invasions and extinctions, may be predicted with assurance.

THE 1973 FLORA

The following lists are based on Moul's compilation of the 1947 Penikese flora (Moul, 1948); species found in both 1947 and 1973 are not repeated. Invasions since 1947 comprise three categories: (1) elements new to Penikese since 1947, (2) re-invasive elements not collected since 1923, and (3) re-invasive elements not collected since 1873. These three groups of species are listed with their habitats in 1973. Those species represented in the 1947 collection but not found in 1973 are listed without habitats; hence future students of the flora will be able, with the aid of this and previous plant lists, to compile a total flora

and to make the sorts of biogeographic comparisons between floras which we have presented earlier. Nomenclature is based on Fernald (1950) unless otherwise noted; the order of the list follows Fernald (1950) for families, treating genera within families and species within genera strictly alphabetically.

Lewis (1920) and later Fogg (1930) in more detail attempted to equate certain species in Jordan's list and absent from the island in 1923 with species present at the latter period. Stuckey and Phillips (1970) accept Lewis's 1924 suggestion and consider Jordan's report of *Lycopus europaeus* on Penikese misleading, citing nonetheless valid reports of *L. europaeus* introduced with ballast in Massachusetts in the late 19th Century. Jordan did not keep voucher specimens and his *Cerastium viscosum* may indeed have been *C. vulgatum,* his *Lycopus europaeus, L. americanus,* etc. Nonetheless, we have encountered five species of vascular plants collected previously only by Jordan, and for the purposes of this listing and in the previous biogeographic computations, have preferred to accept Jordan's identifications at face value, allowing of course for taxonomic revisions and corrections of synonymy. In addition to the 163 species listed, specimens of five other taxa were collected in unidentifiable condition.

All specimens collected in this study have been deposited in the herbarium of Smith College.

Species new to Penikese since 1947:

Distichlis spicata — grasslands behind the marsh
Festuca capillata — grasslands on the west side of the larger section
Panicum clandestinum — around South Pond
Panicum dichotomiflorum — common around Tub Pond
Panicum lanuginosum — rare around Typha Pond
Cyperus erythrorhizos — shore of Typha Pond
Sisyrinchium atlanticum — around Tub Pond

Polygonum pensylvanicum — grasslands near old foundations on the west shore and scattered in depressions on the larger section

Chenopodium ambrosioides — scattered in the tension line on the east side of the larger section

Chenopodium lanceolatum — tension line, just below the grasslands on the west side of the larger section

Chenopodium pumilio (in Gleason, 1952) — tension line on east side of the larger section in the area of South Pond

Ranunculus bulbosus — rare, scattered throughout grasslands

Glaucium flavum — common on the causeway and in the tension line on the southern tip on the main section

Rorippa islandica — near foundations and old stone walls on the eastern side

Oxalis corniculata — scattered in upper grasslands on the larger section

Erodium cicutarium — rare, in the tension line on the east side of the larger section

Geranium robertianum — in the tension line on the eastern side of the larger section

Viola lanceolata — one specimen found on the edge of Tern Pond

Myriophyllum verticillatum — only in Tern Pond

Hedera helix — by the old foundations on the west side

Coelopleurum lucidum — near the marsh

Lycopus rubellus — near Dry Pond and along the edge of Tern Pond

Lycopersicum esculentum — scattered in grasslands and tension line on the east side of the larger section and near Tub Pond

Solanum dulcamara — common in the tension line and around old foundations and stone walls in the upland grasslands

Solanum villosum — in the tension line

Veronica arvensis — uncommon, scattered in tension line

Viburnum dentatum — near the old leprosarium foundations on the west side of the larger section

Cucurbita melo — one plant in a depression near Tub Pond

Aster novi-belgii — common around Typha Pond, on the hill behind the marsh and around the old foundations on the east side

Aster subulatus — edges of the marsh

Cirsium horridulum — scattered in grasslands

Lactuca canadensis — rare, on the causeway

Matricaria matricarioides — common in the tension line

Pluchea purpurascens — common in the marsh

Re-invasive species not collected since 1923:

Setaria lutescens — rare, near Typha Pond

Juncus greenei — common in grassy highlands

Polygonum persicaria — in Dry Pond

Amaranthus retroflexus — in the vicinity of Tub Pond

Portulaca oleracea — near leprosarium foundations

Arenaria peploides — in the beach on the eastern side of the larger section of the island

Spergularia marina — rare, in the beach and tension line on the eastern side of the larger section

Capsella bursa-pastoris — near old foundations on the eastern side of the larger section of the island

Vicia cracca — east shore around old stone walls

Lycopus americanus — near Typha Pond and depressions near Dry Pond

Anthemis cotula — scattered throughout the grasslands over the entire island

Helianthus annuus — one specimen on the causeway

Solidago juncea — not common, scattered in the grasslands behind the marsh and above the tension line

Taraxacum officinale — not common, found in upland grasslands on the larger section of the island

Re-invasive species not collected since 1873:

Digitaria sanguinalis — near Tern Pond, not common

Poa annua — scattered in grasslands on the north end of the larger section

Rumex obtusifolius — east side of the larger section in grasslands just above the tension line

Asclepias incarnata — rare, in grasslands

Gnaphalium uliginosum — rare, on the muddy border of Typha Pond

Species collected in 1947 but not in 1973:

Dryopteris thelypteris, Pinus sylvestris, Ruppia maritima, Andropogon scoparius, Avena sativa, Bromus commutatus, Panicum implicatum, Panicum oricola, Paspalum ciliatifolium, Spartina patens, Carex muhlenbergii, Carex silicea, Cyperus filiculmis, Eleocharis halophila, Eleocharis palustris, Eleocharis parvula, Scirpus americanus, Scirpus paludosus, Scirpus validus, Sisyrinchium angustifolium, Juncus bufonius, Juncus dichotomous, Populus deltoides, Salix pentandra, Quercus rubra, Rheum rhaponticum (Gleason, 1952), *Bassia hirsuta, Ranunculus cymbalaria, Barbarea vulgaris, Brassica juncea, Brassica kaber, Fragaria virginiana, Potentilla argentea, Potentilla egédei, Trifolium hybridum, Trifolium pratense, Vicia angustifolia, Vicia tetrasperma, Euphorbia polygonifolia, Parthenocissus quinquefolia, Parthenocissus tricuspidata, Hypericum mutilum, Kalmia angustifolia, Vaccinium atrococcum, Limosella subulata, Specularia perfoliata, Coreopsis lanceolata, Sonchus oleraceus.*

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LITERATURE CITED

BOYCE, S. G. 1954. The salt spray community. Ecol. Mono. **24**: 29-67.

BURK, C. J. 1968. A floristic comparison of Lower Cape Cod, Massachusetts and the North Carolina Outer Banks. Rhodora **70**: 216-227.

FERNALD, M. L. 1950. Gray's manual of botany: 8th ed. American Book Company, New York.

FLOYD, B. 1932. Strange disappearance of nesting Penikese Island terns. Bird-Banding **3**: 173-174.

FLOYD, C. B. 1933. Further notes from Penikese Island terns. Bird-Banding **4**: 200-202.

FOGG, J. M. 1930. The flora of the Elizabeth Islands, Massachusetts. Rhodora **32**: 119-132, 147-161, 167-180, 208-221, 226-258, 263-281.

GLEASON, H. A. 1952. Illustrated Flora of the Northeastern United States and Adjacent Canada: Vol. 2, Lancaster Press, Inc., Lancaster, Pa.

GOOKIN, W. F. & P. L. BARBOUR. 1963. Bartholomew Gosnold, Discoverer and Planter. Archon Books, Hamden, Connecticut.

HEHRE, E. J., & J. R. CONWAY. 1969. *Glaucium flavum* Crantz from Cape Cod. Rhodora **71**: 540.

HOWLAND, A. F. 1964. Three Islands: Pasque, Nashawena, and Penikese. Privately printed.

JORDAN, D. S. 1874. The flora of Penikese Island. Am. Nat. **8**: 193-197.

KALISCH, P. A. 1972. Tracadie and Penikese: A comparative historical analysis of societal response to leprosy in New Brunswick, 1844-1880 and Massachusetts, 1904-1921. Unpublished manuscript.

KOLATA, G. B. 1974. Theoretical ecology: beginnings of a predictive science. Science **183**: 400-401.

LEWIS, F. I. 1924. The flora of Penikese, fifty years after. Rhodora **26**: 208-221, 226-258, 263-281.

MACARTHUR, R. H. 1972. Geographical Ecology: Patterns in the Distribution of Species. Harper and Row, New York.

————, & E. O. WILSON. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, N. J.

MOUL, E. T. 1948. Flora of Penikese Island. Rhodora **50**: 288-304.

————. 1961. Notes on the flora of Penikese Island, Massachusetts. Rhodora **63**: 149-150.

NISBET, I. C. T. 1973. Terns in Massachusetts: present numbers and historical changes. Bird-Banding **44**: 27-55.

PIKE, R. B., & A. R. HODGDON. 1962. Changes in flora of the Machias Seal Islands. Rhodora **64**: 340-346.

PRESTON, F. W. 1962. The canonical distribution of commonness and rarity. Ecology **43:** 185-215, 410-432.

RICH, P. H. 1973. Penikese Island pond data. Unpublished manuscript.

SEYMOUR, F. C. 1969. The Flora of New England. C. E. Tuttle Co., Rutland, Vt.

SIMPSON, G. G. 1965. The Geography of Evolution. Chilton Company, Philadelphia, Pa.

STUCKEY, R. L., & W. L. PHILLIPS. 1970. Distributional history of Lycopus europaeus (European water-horehound) in North America. Rhodora **72:** 351-369.

WILLIS, E. O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. Ecol. Mono. **44:** 153-169.

ZINN, D. J., & J. S. RANKIN. 1952. Fauna of Penikese Island, 1947. The Kendall Printing Company, Falmouth, Mass.

————, & S. J. KAHN. 1972. Geology and geography of Penikese Island. Trans. Conn. Acad. Arts and Sci. **44:** 429-436.

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SOMATIC CHROMOSOME NUMBERS FOR SOME NORTH AMERICAN SPECIES OF JUNCUS L.

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The genus *Juncus* is worldwide in distribution and comprises something over 200 species. Chromosome numbers have been determined for less than half the species and, while chromosome numbers alone cannot serve to distinguish species, it seems likely that knowledge of chromosome numbers will serve in some instances to supplement taxonomic judgments made largely on morphological grounds.

MATERIALS AND METHODS

All chromosome counts reported here were obtained from squashes of root tips from plants in the field or from plants maintained in moist sand in the greenhouse. Excised root tips were pretreated for one hour in 0.1% colchicine, fixed in 3:1 absolute ethanol: glacial acetic acid, hydrolyzed for ten minutes at 60°C in *N* HCl, and stained in Schiff's Reagent. With this treatment, the chromosomes in all species were between one and 1.5 micrometers in length, as measured with an ocular micrometer under oil immersion. Because of the size of the chromosomes, no observations could be made as to centromere position, satellites, or secondary constrictions. The counts were repeatedly verified in several different root tips from the population. Voucher specimens with a drawing of the chromosomes were prepared. A complete set of vouchers is deposited here at the Herbarium, University of Wisconsin-Oshkosh, and some duplicate vouchers have been distributed elsewhere.

We had intended at the outset to fix the root tips without pretreatment, so that our findings would be comparable to those of Snogerup (1963), who made many observations on relative sizes of chromosomes within the genome of a species. However, we encountered so many difficulties in

getting countable metaphase figures that we resorted to colchicine pretreatment, which shortens chromosomes and makes it impossible for us to characterize the chromosomes with respect to relative lengths.

OBSERVATIONS

We adopt here, without comment, the sectional designations used by Snogerup (1963) and largely by Fernald (1950).

I. Section Poiophylli:

1. **J. bufonius** L. WISCONSIN, WINNEBAGO CO.: along south side of RR tracks at crossing on state route 110, Algoma Blvd., at the N city limits of Oshkosh, sect. 10, T18N, R16E. *Harriman* 9207. 10 July, 1973. $2n =$ ca. 108. An array of chromosome numbers has been reported for this species (see, e.g., Löve & Löve, 1961). It remains to be demonstrated whether morphological correlations with these various chromosome numbers exist. Because this annual species regularly sets seeds, despite the high chromosome numbers that have been demonstrated in some populations, and because these higher polyploids are doubtless autopolyploids, it may well be that at least some populations of the species are agamospermous. The observations of Marie-Victorin & Rouleau (1964) on pollination in this species do not, of course, preclude the possibility of agamospermy.

2. **J. compressus** Jacq. WISCONSIN, WINNEBAGO CO.: along grassy edge beneath U.S. 41 overpass at state route 21, on the south side of route 21 only, and on to the lawn at the Howard Johnson's, Oshkosh. *Harriman* 10186. 11 July, 1974. $2n = 44$. This count is in agreement with that reported in Snogerup (1963) and repeated in Nilsson & Snogerup (1971) and is the first report for this species from New World material; the report of $2n = 40$ (Holmen *in* Löve & Löve, 1961) has not been confirmed thus far.

is primarily Eurasian species is reported to range in rth America (perhaps as an introduction) from New- ndland and Nova Scotia to eastern Ontario. This is the t report of its occurrence in Wisconsin; duplicates of it ve been distributed to WIS, UWM, MIL, MICH, NY, GH, U, NHA, MIN, USFS, and elsewhere. The plants occur y densely by the hundreds, in sandy clay or clay alone, full sun as well as in partial shade cast by the concrete rpass bridge. In aspect, they are a deep green-black or, not at all glaucous as characterized by Fernald 50, p. 403). The plants were abundantly in fruit and dily identifiable in the treatments of Fernald (*op. cit.*), of Nilsson & Snogerup (1971, 1972). Dr. F. J. Her- nn has kindly confirmed the identification, and has en permission to publish two further records for the cies which considerably extend its heretofore known ge: MONTANA, BEAVERHEAD CO.: marshy edge of road- ditch, 9 miles south of Wisdom. *Hermann* 12484. eptember, 1955. (CA, MONT, US) and, COLORADO, MER CO.: sedge meadow south of Spring Canyon, 5 s southwest of Fort Collins. *Herman* 23841. 27 June, . (COLO, NY, USFS). Dr. Askell Löve has most help- called to my attention reports of *J. compressus* for itoba by Scoggan (1957).

. dichotomus Ell. FLORIDA, ALACHUA CO.: grassy , bottom of steep embankment, at a rest stop on north- nd I-75, just south of its junction with state route 121. *riman* 8860. 20 April, 1973. $2n = 80$. A chromosome ber for this species has not heretofore been published; ies to which it is closely allied, e.g., *Juncus Dudleyi*, *reenei*, and *J. interior*, likewise have $2n = 80$ (see v).

. Dudleyi Wieg. WISCONSIN, WINNEBAGO CO.: sand t junction of state route 116 and county trunk E, sec- 19, T18N, R15E. *Redmond* 139. 2 July, 1971. $2n =$ he first report of a number for this species.

5. **J. Greenei** Oakes & Tuckerm. WISCONSIN, WAUSH. CO.: very abundant in a mushy roadside ditch at the ju tion of county trunk N and state route 21 at the east limits of Redgranite, section 17, T18N, R12E. *Harrin* 9258. 17 July, 1973. $2n = 80$, the first number to be p lished for this species.

6. **J. interior** Wieg. WISCONSIN, ADAMS CO.: open, dry sands, on a sand lane that dead-ends at Peten Flowage, west ca. 100 yds. off county trunk Z at Arc Lane, section 15, T20N, R5E. *Harriman* 10095. 29 J 1974. $2n = 80$, the first report of a chromosome num for this species. The status of this species is a matte some debate; Correll & Johnston (1970) suggest that probably conspecific with *Juncus dichotomus;* altho they do not reduce it to the synonymy of that species, chromosome numbers reported here would permit suc decision. It is obvious that *J. interior* is closely relate *J. tenuis* as well; indeed, the two are commonly mislabe in herbaria. However, despite the strong morpholog similarity between these two taxa, the chromosome n bers of North American populations thus far studied below for *J. tenuis*) would not support reducing *J. inte* to the synonymy of *J. tenuis*.

7. **J. tenuis** Willd. WISCONSIN, WINNEBAGO CO.: sand at junction of state route 116 and county trunk E, sec 19, T18N, R15E. *Redmond* 140. 2 July, 1971. $2n =$ This determination agrees with that of Taylor & Mull (1968). The reports of $2n = 30$ (Löve & Löve, 1948) $2n = 32$ (Sasaki, 1937) suggest an aneuploid reducti series in this very widespread species. The report of 2 84 (Nilsson & Snogerup, 1971), presumably from Sca navian plants, is anomalous at present, but suggests existence of various chromosomal races which ma correlated with morphological characters.

II. Section Genuini:

J. balticus Willd. WISCONSIN, WAUSHARA CO.: mar-
ns of Plainfield Lake, section 18, T20N, R9E. *Redmond*
35. 22 July, 1971. $2n = 80$, apparently the first report
or a New World population of this widespread species.
ublished reports include $2n = 40$ (Löve & Löve, 1956)
nd $2n = 80$ (Löve & Löve, 1961). Since there are ap-
arently both diploid and (auto) polyploid races, detailed
ytotaxonomical investigation is warranted here.

. **J. effusus** L. WISCONSIN, MARQUETTE CO.: Germania
Iarsh, section 12, T16N, R10E, in moist roadside sands.
Redmond 115. 26 September, 1970. $2n = 40$. The same
umber has been reported by Löve & Löve (1961), but
Taylor & Mulligan (1968) report $n = 40$ for var. *gracilis*
Hook. The voucher for the present determination will key
o var. *Pylaei* (LaHarpe) Fern. & Wieg., in Fernald's key
(1950). However, we agree with Voss (1972) that, "While
the extremes of variation are well marked, too many inter-
mediate plants occur to make it useful to attempt to dis-
tinguish varieties here." It may be that extensive chromo-
some counting over a considerable portion of the range of
this species will reveal chromosomal differences among the
morphological "varieties" that will lead to a more workable
delimitation of infraspecific categories in this species.
Snogerup (1963) reports $2n = 42$ for a number of Swed-
ish populations of this species. It appears that both eu-
ploidy (from diploid to tetraploid levels) and aneuploidy
(at the diploid level) are at work in this species; it re-
mains to be demonstrated whether the complex variability
of this species can be correlated with chromosome numbers.

10. **J. filiformis** L. WISCONSIN, WOOD CO.: abundant, hundreds of clumps, in the second bog to the east of the pump house, in the Getzin cranberry bog, east off county trunk Z, ½ mile south of the junction of Z and state route 73, section 14, R5E, T21N. *Harriman* 10169. 29 June, 1974. $2n = 70$. Previous reports of chromosome numbers

for this species include $2n = 40$ (Löve & Löve, 1956) ar $2n =$ c. 80 (Jørgensen et al., 1958). The report here $2n = 70$ is anomalous in a genus where diploid numbe are overwhelmingly 40 and 80, but we determined it r peatedly from many root tips in the population cited. Lik so many other species of *Juncus*, this species appears to b evolving both by euploidy and aneuploidy, but in th instance with the aneuploidy occurring at the tetraploi level (from 80 down to 70) rather than at the diploid leve To judge from the manual treatments of this species, ther is relatively little variability and apparently little or n taxonomic confusion surrounding this species, despite th various chromosome numbers.

11. **J. inflexus** L. MICHIGAN, HOUGHTON CO.: roadside and in the ditch, beside southbound U.S. 41, ca. 50 yds inside the Hancock city limits, and 100 yds. downhill from the scenic overlook. *Harriman* 9682. 2 September, 1973 $2n = 40$, the first report for a New World population of this species; the number is in agreement with other published reports for the species (Löve & Löve, 1961; Snogerup, 1963).

III. Section Graminifolii:

12. **J. biflorus** Ell. MISSOURI, WARREN CO.: along a drainage course from artificial ponds on the Hartman farm on state route 47, just south of its junction with county highway CC, south of Warrenton. *Harriman* 9349. 11 August, 1973. $2n = 40$, apparently the first number to be published for this species.

13. **J. marginatus** Rostk. WISCONSIN, MARQUETTE CO.: in black muck, edge of a small puddle, off Duck Creek Avenue, section 26, R10E, T17N. *Redmond* 382. 11 August, 1971. $2n = 40$; Snogerup (1963) reported $2n = 38$, his voucher from near Washington, D.C. These two species, *Juncus biflorus* and *J. marginatus*, are clearly very

closely related, together with *J. Longii* Fern., whose chromosome number is unknown. Snogerup argues that both *J. biflorus* and *J. Longii* should be reduced to the synonymy of *J. marginatus;* the known chromosome numbers lend no support to maintaining them as distinct species. Nonetheless, all current manuals of eastern North American plants maintain these as distinct entities.

IV. Section Septati:

14. **J. acuminatus** Michx. WISCONSIN, WAUSHARA CO.: wet sand at the very edge of the water, north shore of Taylor Lake, SE¼ section 29, R12E, T19N. *Harriman* 10319. 27 July, 1974. $2n = 40$. And: MISSOURI, WARREN CO.: around artificial ponds, in heavy clay, on the Hartman farm on state route 47, just south of its junction with county highway CC, south of Warrenton. *Harriman* 9345. 11 August, 1973. $2n = 40$. These are apparently the first reports of a chromosome number for this species.

15. **J. alpinus** Vill. WISCONSIN, GREEN LAKE CO.: marsh beyond the east end of Water Street, in the village of Princeton. *Harriman* 2579. 3 October, 1967. $2n = 40$, apparently the first determination for this species from continental North America; the same number has been reported for Greenland material (Jørgensen et al., 1958), European material (Löve & Löve, 1961), and Queen Charlotte Islands plants (Taylor & Mulligan, 1968). A count of $2n = 80$ for subsp. *nodulosus* (Wahlenb.) Hulten by Vaarma et al. (*in* Löve & Löve, 1948) again demonstrates the occurrence of (auto)polyploidy in various Junci.

16. **J. articulatus** L. MICHIGAN, SCHOOLCRAFT CO.: roadside marshy ditch, in black, peaty muck, at entrance to Seney National Wildlife Refuge, on state route 77, section 16, Germfask Township. *Harriman* 10486. 24 August, 1974. $2n = 80$, again an apparent first determination for this species from continental North America. The same

chromosome number has been determined for the species elsewhere (Löve & Löve, 1961; Taylor & Mulligan, 1968, where it is asserted that the reports of $2n =$ ca. 60 and $n =$ ca. 30 by Wulff (1937 and 1938, respectively) should be referred to another species.) This species is somewhat confluent with *J. alpinus;* the characters given in Hitchcock et al. (1969) serve best to distinguish the two.

17. **J. brachycarpus** Engelm. MISSOURI, MONTGOMERY CO.: abundant in low, abandoned, waste edge of a soybean field on the Welch farm, beside I-70, at the north edge of the village of Jonesburg. *Harriman* 10455. 6 August, 1974. $2n = 44$, the first report for this species. Like *J. compressus,* where both $2n = 40$ and $2n = 44$ have been reported, *J. brachycarpus* may prove to be made up of more than one chromosomal race, when more populations from throughout its extensive range have been sampled.

18. **J. brachycephalus** (Engelm.) Buch. WISCONSIN, WAUSHARA CO.: in marly muck at a boat landing on Marl Lake, section 23, T19N, R9E. *Harriman* 7589. 28 August, 1971. $2n = 80$, the first report for this species.

19. **J. brevicaudatus** (Engelm.) Fern. WISCONSIN, PORTAGE CO.: in sand pits beside U.S. 51 at the north city limits of Stevens Point, section 18, T24N, R8E. *Redmond* 245. 13 July, 1971. $2n = 80$; this determination confirms the reports of $2n = 80$ by Löve & Löve (1966), Löve & Ritchie (1966), and Snogerup (1963).

20. **J. canadensis** J. Gay in La Harpe. WISCONSIN, MARQUETTE CO.: sandy, wet roadside ditch in Germania Marsh, section 12, T16N, R10E. *Redmond* 114. 26 September, 1970. $2n = 80$; the same number has been determined for this species by Snogerup (1963). It is to be expected that these three species, *Juncus brachycephalus, J. brevicaudatus,* and *J. canadensis,* which are somewhat confluent morphologically, would all have the same chromosome number.

. **J. nodosus** L. WISCONSIN, GREEN LAKE CO.: at edge a drainage ditch in a marsh east beyond the end of East ater Street, near the airport, in Princeton. *Harriman* 78. 3 October, 1967. $2n = 40$, apparently the first re-rt of a chromosome number for this species.

. **J. pelocarpus** E. Meyer. WISCONSIN, MARQUETTE CO.: very edge of water in wet sand, on Tuttle Lake at Camp dian Sands, section 22, T17N, R10E. *Redmond* 411. 11 ugust, 1971. $2n = 40$, apparently the first report of a romosome number for the species.

. **J. rugulosus** Engelm. CALIFORNIA, LOS ANGELES CO.: et ditch and side of small creek along rough gravel por-on of San Francisquito Canyon Road, 15 miles north of ugus, at possibly 1500 feet elevation, or lower; rhizomes ngled and knotted. *Parfitt* 1060. 27 July, 1974. $2n = 40$, e first report for this species.

. **J. Torreyi** Cov. WISCONSIN, WINNEBAGO CO.: very undant in marshy area between Soo Line and C&NW R tracks, ca. 100 yds. north of the junction of county unks Y and A, section 30, R17E, T19N. *Harriman* 2574. September, 1967. $2n = 40$; Snogerup (1963) likewise termined the same number for plants from eastern Can-a. This species is similar to *J. nodosus* L., but almost ways readily separable; we had expected to find *J. Tor-yi* to be a polyploid derivative of *J. nodosus*, since *J. rreyi* differs primarily in being larger in all its parts an *J. nodosus*.

V. Section Ensifolii

. **J. ensifolius** Wikstr. WISCONSIN, ASHLAND CO.: adside ditch, in standing water over a substrate of anite chips and mud, on the east side of state route 13, actly 0.5 mile south of the Mellen city limits, section 6, 4N, R2W, very abundant. *Harriman* 7484. 16 August, 71. $2n = 40$; this determination agrees with the numer-s reports of Taylor & Mulligan (1968) and Snogerup

(1963). The occurrence of this species in Wisconsin d serves comment: the population was discovered by Hug Iltis at WIS and he very kindly shared his discovery wit us; its establishment in this single locality in Wisconsi is unexplained. The population comprised several hundre of flowering stems, all abundantly in fruit and producin apparently viable seeds; since similar moist habitats occu throughout much of the northcentral United States ar adjacent Canada, the species will doubtless be found occupy a much more extensive range in eastern Nort America in the future. (The species is mentioned in Mari Victorin & Rouleau (1964) as occurring in Quebec.)

SUMMARY OF SOMATIC CHROMOSOME NUMBERS REPORTEI HERE, AND BASE NUMBERS IN THE SECTIONS OF JUNCUS

Sect. Genuini (Buchenau) Vierhapper : $x = 20$ and 2

1. *J. balticus* 80
2. *J. effusus* 40
3. *J. inflexus* 40

These numbers support Snogerup's designation (1963) this section as having $x = 20$.

Sect. Poiophylli (Buchenau) Vierhapper : $x = 20$, 2 and 22

1. *J. bufonius* ca. 108
2. *J. compressus* 44
3. *J. dichotomus* 80
4. *J. Dudleyi* 80
5. *J. Greenei* 80
6. *J. interior* 80
7. *J. tenuis* 40

We ignore *J. bufonius* in calculating base numbers, sin the numerous counts on this species fit into no definab pattern; the data reported here permit adding the ba number 20 to this very diverse section of the genus.

Sect. Graminifolii (Buchenau) Vierhapper : $x = 19$ and 20

1. *J. marginatus* 40
2. *J. biflorus* 40

Snogerup (1963) calculated a base number of 19 for this section, based on his one count of $2n = 38$ for *J. marginatus*. The counts reported here establish a second base number for this section.

Sect. Septati (Buchenau) Vierhapper : $x = 20$ and 22

1. *J. acuminatus* 40
2. *J. alpinus* 40
3. *J. articulatus* 80
4. *J. brachycarpus* 44
5. *J. brachycephalus* 80
6. *J. brevicaudatus* 80
7. *J. canadensis* 80
8. *J. nodosus* 40
9. *J. pelocarpus* 40
10. *J. rugulosus* 40
11. *J. Torreyi* 40

The counts reported here generally support Snogerup's designation of base number in this section as $x = 20$; however, the count for *brachycarpus* now establishes a base number of $x = 22$ in this section as well.

Sect. Ensifolii Rydb. ex Snogerup : $x = 20$

1. *J. ensifolius* 40

The count reported here for a Wisconsin population of the species confirms this base number for the section.

LITERATURE CITED

CORRELL, D., & M. JOHNSTON. 1970. Manual of the Vascular Plants of Texas. Texas Research Foundation, Renner. 1881 pp.

FERNALD, M. L. 1950. Gray's Manual of Botany. 8th Edition. American Book Co., New York. 1632 pp.

HITCHCOCK, C. L. 1969. Juncaceae. *In:* Hitchcock, C. L., et al., "Vascular Plants of the Pacific Northwest." Univ. Wash. Publ. Biol. **17** (1): 179-219.

JØRGENSEN, C., et al. 1958. The flowering plants of Greenland. A taxonomical and cytological survey. Biol. Skr. Dansk. Vidensk. Selsk. **9**: 1-172.

LÖVE, A., & D. LÖVE. 1948. Chromosome numbers of northern plant species. Icel. Univ. Inst. Appl. Sci. Dept. Agr. Rep. B. **3**: 1-131.

__________. 1956. Cytotaxonomical conspectus of the Icelandic Flora. Acta Hort. Gotob. **20**: 65-291.

__________. 1961. Chromosome numbers of central and northwest European plant species. Op. Bot. (Lund) **5**: 1-581.

__________. 1966. Cytotaxonomy of the alpine vascular plants of Mt. Washington. Univ. Colo. Studies, Ser. Biol. **24**: 1-74.

__________, & J. C. RITCHIE. 1966. Chromosome numbers from central Canada. Canad. Jour. Bot. **44**: 429-439.

MARIE-VICTORIN, & E. ROULEAU. 1964. Flore Laurentienne. University of Montreal Press. 925 pp.

NILSSON, O., & S. SNOGERUP. 1971. Drawings of Scandinavian Plants. 60-64. *Juncus* L. Bot. Not. **124**: 435-441.

__________. 1972. Drawings of Scandinavian Plants 75-80. *Juncus* L. Bot. Not. **125**: 203-211.

SASAKI, M. 1937. Chromosome numbers of Miscanthus and Juncaceous plants. Jap. J. Genet. **13**: 260.

SCOGGAN, H. J. 1957. Flora of Manitoba. National Museum of Canada, Bulletin No. 140, Biological Series No. 47. 619 pp.

SNOGERUP, S. 1963. Studies in the genus *Juncus*. III. Observations on the diversity of chromosome numbers. Bot. Not. **116**: 142-156.

TAYLOR, R., & G. MULLIGAN. 1968. Flora of the Queen Charlotte Islands. Pt. 2. Cytological aspects of the vascular plants. Canada Dept. of Agriculture, Monograph No. 4, part 2. 148 pp.

VOSS, E. 1972. Michigan Flora. Pt. 1. Gymnosperms and Monocots. Cranbrook Inst. of Science, Bulletin 55. 488 pp.

WULFF, H. G. 1937. Karyologische untersuchungen an der Halophyten flora Schleswig-Holsteins. Jahrb. Wiss. Bot. **84**: 812-840.

__________. 1938. Chromosomen studien an der schleswig-holsteinischen Angiospermen-Flora. II. Ber. Deutsch. Bot. Ges. **56**: 247-254.

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MORPHOLOGICAL VARIATION OF ELODEA IN WESTERN MASSACHUSETTS: FIELD AND LABORATORY STUDIES

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The genus *Elodea* Michaux (Helobiae: Hydrocharitaceae) consists of 17 species, nine of which are distributed in North America and eight in South America. In North America *E. canadensis* Rich. in Michx. is the most widespread species, spanning the continent from Quebec to British Columbia, south to Alabama and California. *Elodea nuttallii* Planch. has the second widest range, occurring abundantly from the lowlands in Maine to North Carolina, west to Missouri, and also in Idaho. Other North American species are extremely restricted in range or are known only from single localities. Neither *E. canadensis* nor *E. nuttallii* has been reported in South America (St. John, 1965).

Elodea canadensis and *Elodea nuttallii* are economically important plants because of their frequent occurrence as troublesome waterweeds. Studies indicate that these two species are present at different stages in the eutrophication of a lake and that *E. nuttallii* may have a greater tolerance to various forms of pollution, including nutrient enrichment, than *E. canadensis* (Stuckey, 1971; Lind and Cottam, 1969; Volker and Smith, 1965).

Plants of both *Elodea canadensis* and *E. nuttallii* are dioecious. The flowers of the two species differ primarily in size. Those of *E. canadensis* are larger, and at flowering both the staminate and pistillate flower buds are raised by filiform hypanthia to the water's surface where anthesis and pollination take place. Pistillate flowers of *E. nuttallii* are also raised by elongation of the hypanthium, but staminate flowers of this species are sessile. Just prior to anthesis the staminate flowers abscise and float to the surface of the water, where they open. Their pollen is shed on the surface of the water and floats to the pistillate flowers (St. John, 1965).

Pollination and seed formation are extremely rare. Reasons for this are the brief and infrequent flowering periods and the differing abundance of the two sexes in nature, pistillate plants being collected much more often than staminate plants. At nearly every locality of staminate plants, pistillate plants are known to occur also, although the reverse is not true.

A distinction has often been made between pistillate and staminate plants of *Elodea canadensis* to the extent that the staminate plants were at one time believed to represent a separate species. Staminate flowers differ from pistillate ones in having longer sepals and petals. The leaves of successive nodes on the holotype and on most of the staminate plants which St. John examined (1965) were more widely spaced, narrower, and thinner than those of pistillate plants. However, in some collections of flowering staminate plants, the broad, firm, imbricate leaves were indistinguishable from those of pistillate plants (St. John, 1965). The distinction between male and female plants on the basis of vegetative morphology alone is, therefore, neither valid nor dependable.

Due to the brief flowering period, the minute size of the flowers and infrequent flowering, leaf size, shape, and arrangement are often the only criteria available to differentiate species. The vegetative phase of *Elodea* is submerged, and both *E. canadensis* and *E. nuttallii* grow either rooted in the bottom or free-floating. Plants of *Elodea canadensis* have a firm, dark green appearance, with ovate to oblong leaves crowded and densely imbricated near the apex. *Elodea nuttallii* plants are slenderer, pale green, and flaccid, with linear or narrowly linear lanceolate leaves. Table 1 gives ranges and some averages of leaf widths of *E. canadensis* and *E. nuttallii* published in recent treatments. Leaf length of both species is in the range of 6-17 mm (Fernald, 1950).

Problems of misidentification of species of *Elodea*, particularly *E. canadensis* and *E. nuttallii*, appear to be compounded by phenotypic plasticity in the vegetative or-

ans of the plant. Additionally, the superficial similarity of he vegetative state of *Egeria densa* Planch. (once treated s *Elodea canadensis* var. *gigantea;* see St. John, 1965, and Iarie-Victorin, 1931) to that of *Elodea* spp. has introuced errors in reports of chromosome counts, habit decriptions and range delineations due to misdeterminations.

Vegetative reproduction in both species is the primary neans of regeneration. The brittle and delicate stems are asily fragmented by currents, winds, motorboat traffic, oraging animals, or other disturbance. Any part of the xis is capable of producing a new plant if a dormant ateral bud is present and the fragment does not become esiccated (Sculthorpe, 1967). Fragments can become ooted in new locations by means of adventitious roots roduced at the nodes.

Reductions of leaf width in *Elodea canadensis* in reponse to nutrient enrichment have been reported (Adams t al., 1971). Preliminary observations of the vegetative rowth of *E. canadensis* and *E. nuttallii* raised in tanks

TABLE 1

Ranges and averages of leaf widths of *Elodea canadensis* nd *Elodea nuttallii* in recent treatments.

uthor	*E. canadensis*	*E. nuttallii*
'ernald (1950)	1.0-5.0 mm	0.3-1.5 mm
t. John (1965)	1.0-5.0 mm	0.3-1.5 mm
ivingston (1967)	2.0-5.0 mm	1.2-1.5 mm
eymour (1969)	1.0-5.0 mm	0.3-1.5 mm
adford et al. (1964)	1.0-5.0 av. 2.0 mm	≤ 1.5 av. 0.3 mm
leason (1952)	1.2-4.0 av. 2.0 mm	0.7-1.8 av. 1.3 mm
'assett (1969)	1.2-4.5 av. 2.0 mm	0.7-1.8 av. 1.3 mm
Iuenscher (1944)	1.2-4.0 av. 2.0 mm	0.7-1.8 av. 1.3 mm

at higher temperatures than normally encountered in t
field revealed morphological variation in *E. canadens*
An experiment was therefore devised to determine t
extent of this morphological change in vegetative plar
induced by growing specimens at various temperatur
The study also attempted to determine whether accept
taxonomic criteria for distinguishing *E. canadensis* a
E. nuttallii are effective in natural populations.

Effects of Elevated Temperature on the Vegetative Morphology of Elodea canadensis

MATERIALS AND METHODS

Plants of *Elodea canadensis* were collected from Bro
Brook near its entry into Nashawannuck Pond, Eastham
ton, Massachusetts. Water temperatures in Broad Broo
which is fed in part by natural artesian wells, were mea
ured at biweekly intervals during summer, 1973, at t
collection site. Mean temperature in Broad Brook w
13.5 C. No readings deviated more than one degree Cen
grade from the mean. Plants were removed from t
collecting site at the substrate level, placed in gallon ja
filled with pond water for transport to the Lyman Pla
House at Smith College, briefly rinsed with tap wate
and cut to 8 cm lengths. Each 8 cm piece had a growi
tip and was without branches or roots.

Eight 5.7 liter (6 qt.), all glass, rectangular aquar
were used for culture. Sand 4-6 cm deep was placed
each tank, and the tanks were filled with water fro
Broad Brook. Twenty-five 8 cm plants were placed in ea
tank with the lower portions of the stem embedded in t
sand. The tanks were marked and placed in a water ba
with non-transparent sides which shaded them so that, f
the most part, plants received light only through the su
face of the water.

All growth experiments were conducted in the Lyman Plant House, where plants received natural day lengths and were subject to day-night and day-to-day temperature fluctuations. Water lost through evaporation was replaced. Daytime temperatures ranged from 19 C to 30 C with a mean of 25.6 C.

Plants were harvested, measured, and pressed at intervals of 1 week, 2 weeks, 4 weeks, 5 weeks, and 7 weeks. Fifteen plants were measured each time except week 5, when by error six were measured. Since the measuring process destroyed the plants, five additional specimens were pressed and reserved as vouchers each week. These were deposited in the herbarium of Smith College. Parameters measured were length, weight, whorls/2 cm, width of leaves, and length of leaves. Ten leaves were removed from each plant and measured with a millimeter ruler. On plants 1 week old, the first five leaves measured were from the area of the original 8 cm of the plant. The rest were spaced evenly up the newly grown portion of the stem. In following weeks, the procedure was the same except only three of the leaves measured were from the original section of the plant. The experiment began July 2, 1973, and the final measurements were taken August 20, 1973.

DISCUSSION

The number of leaves having widths less than or equal to 1.5 mm increased on cultured specimens of *Elodea canadensis* as the experiment progressed (Table 2). Regression analysis (Sokal and Rohlf, 1969) of the relationship between number of leaves 1.5 mm or less in width and age in weeks reveals a highly significant positive regression ($.02 > P > .01$).

Plants grown in Broad Brook under field conditions at an average temperature of 13.5 C represent the control group. These specimens of *Elodea canadensis* did not show a change in leaf size. Mean width of leaves was 2.62 mm with a range of 2.0-4.0 mm.

Leaves produced in culture tended to resemble *Elodea nuttallii*. This effect was more pronounced during later phases of the experiment. Leaves on the original 8 cm of each plant retained their initial dimensions (3-4 mm). Leaves produced above them were narrower (2-3 mm), and this area of intermediate-sized leaves was followed by a portion of stem having very short, narrow leaves (1.75-2.25 mm). All growth above that section consisted of longer, more narrow leaves (1.25-1.75 mm). Leaves produced in culture were paler green and more flaccid than those present at the beginning of the experiment.

MORPHOLOGICAL VARIATION IN SELECTED POPULATIONS OF ELODEA IN WESTERN MASSACHUSETTS

MATERIALS AND METHODS

Elodea plants were sampled at 20 localities throughout western Massachusetts. Publications No. 10-2 (McCann and Daly, undated), No. 10-4 (McCann and Daly, 1972), and No. 11 (Livingston and Bentley, undated) of the Water Resources Research Center at the University of Massachusetts were used as guides to the location of possible collection sites.

A single measurement of water temperature was made at each site. Temperatures varied from 13 C at Broad Brook to 33 C at Buck Pond. At 11 sites, water temperatures were 25 C or higher at the time of collection.

Collected plants were placed in labeled jars with pond water. Plants were rinsed, cut into 8 cm pieces, and weighed. The number of whorls per 2 cm length, and the length and width of five leaves on each of 20 plants were measured in all but three populations in which only ten plants were available for measurement.

Collections were made from July 3 to September 16, 1973.

TABLE 2

Percent of total number of leaves measured which had a width $\leq$ 1.5 mm on specimens of *Elodea canadensis* at times before and during culture.

Weeks in Culture	Percent of leaves $\leq$ 1.5 mm
0	0
1	3.3
2	19.3
4	28.0
5	30.0
7	37.3

DISCUSSION

All plants collected occurred in water not more than 1.5 meters deep. Characteristic habitats were silt, sand on silt, and sand substrates in water of slow to moderate current velocity. Lakes where *Elodea* was found had open water, were heavily used by man in most cases, and had moderate aquatic vegetation cover. Isolated lakes with little submergent vegetation, rocky bottoms, and limited use did not support *Elodea,* nor did highly eutrophic lakes with little open water and thick covers of *Nymphaea odorata, Nuphar variegatum, Pontederia cordata,* and *Lemna minor.* Sites where plants were collected varied from clean, clear water to polluted, turbid conditions.

Leaf length of *Elodea canadensis* and *E. nuttallii* are generally described as similar (St. John, 1965; Fernald, 1950); hence only leaf width was used to differentiate species. Table 3 is a list of the collection sites, their location by town, and the range, 95% confidence interval, and mean of the leaf width of each population. Two level nested anova (Sokal and Rohlf, 1969) reveal a highly significant variation among the 20 populations ($P \leq .001$), and a non-significant variation among individual plants within a population. The samples clearly fall into two

groups. Card Pond, Prospect Lake, Broad Brook, and Lake Buel form one group; their mean leaf widths are all greater than 2.5 mm, and their ranges do not extend below 2 mm. On this basis, these four should be classified as *E. canadensis* (see Table 1). Flowers characteristic of *E. canadensis* were produced by plants of the Broad Brook population in culture. None of the areas where these four populations were collected exhibited such overt signs of pollution as high turbidity, foul odor, oil scum, or algal bloom.

TABLE 3

Collection site, location by town, and mean, 95% confidence interval and range of leaf width for 20 populations of *Elodea* collected in western Massachusetts.

Collection Site	Location by Town	Mean and Confidence Interval	Range
Prospect Lake	Egremont	3.31 ± 0.18	2.50-4.00
Card Pond	West Stockbridge	3.19 ± 0.25	2.25-4.75
Lake Buel	Monterrey	2.99 ± 0.14	2.00-4.00
Broad Brook	Easthampton	2.62 ± 0.18	2.00-4.00
Harts Brook	Hadley	1.75 ± 0.13	1.50-2.25
Chapin Pond	Ludlow	1.67 ± 0.06	1.25-2.00
Benton Pond	Otis	1.63 ± 0.08	1.25-2.00
Lake Garfield	Monterrey	1.54 ± 0.18	1.00-2.50
Ashley Pond	Holyoke	1.44 ± 0.08	1.25-2.00
Porter Lake	Springfield	1.43 ± 0.06	1.00-1.75
Congamond Lake	Southwick	1.42 ± 0.09	1.00-2.00
Hulbert's Pond	Northampton	1.34 ± 0.11	1.00-1.75
Pequot Pond	Westfield	1.29 ± 0.05	1.00-1.75
Center Pond	Becket	1.25 ± 0.13	1.00-2.00
Manhan River	Southampton	1.23 ± 0.07	1.00-1.50
Paradise Pond	Northampton	1.22 ± 0.06	1.00-1.50
Nashawannuck Pond	Easthampton	1.20 ± 0.08	1.00-1.75
Forge Pond	Granby	1.18 ± 0.05	1.00-1.50
Buck Pond	Westfield	1.11 ± 0.04	1.00-1.50
Norwich Pond	Huntington	1.03 ± 0.03	1.00-1.50

Twelve of the sample populations have mean leaf widths of less than 1.5 mm: Hulbert's Pond, Forge Pond, Ashley Pond, Porter Lake, Congamond Lake, Buck Pond, Center Pond, Pequot Pond, Manhan River, Nashawannuck Pond, Paradise Pond, and Norwich Pond. Flowers typical of *Elodea nuttallii* were observed in the Hulbert's Pond, Nashawannuck Pond, and Paradise Pond populations. On the basis of their leaf widths, these are apparently *E. nuttallii.* Several of these 12 populations of *E. nuttallii,* including Hulbert's Pond and Nashawannuck Pond have ranges extending beyond the 1.5 mm limit, and three exceed the 1.8 mm limit set by some authorities.

Four populations remain unclassifiable: Chapin Pond, with mean leaf width 1.67 mm; Lake Garfield, 1.54 mm; Benton Pond, 1.63 mm; and Harts Brook, 1.75 mm. Flowering was not observed in any of these populations. It is conceivable that flowers are not as definitive a taxonomic criterion as is supposed, most herbarium specimens being based on strictly vegetative material (Radford et al., 1964), and *Elodea canadensis* and *E. nuttallii* may not be as clearly differentiated as presumed. Fertile crosses of *E. canadensis* with *E. nuttallii* have been reported (Ernst-Schwarzenbach, 1945), and these unclassifiable populations may be of hybrid origin. These four populations could represent another previously undescribed species or one of the other species of limited distribution outside its known range. They may also be specimens of *E. canadensis* with decreased leaf width as a response to environmental conditions. Chromosome counts will not aid in species identification, because diploid numbers overlap and seem to vary (Radford et al., 1964; Darlington and Ammal, 1945; Santos, 1924).

SUMMARY

Elodea canadensis and *E. nuttallii* are economically important plants because of their occurrence as troublesome waterweeds and their potential use as indicators of pollution. Due to infrequent and brief flowering, leaf morphol-

ogy is often used to differentiate species. In an experimen designed to test the effects of elevated temperature on th vgetative morphology of *E. canadensis*, leaf width wa reduced, and leaves were produced which fell within th reported range of *E. nuttallii*. Accepted taxonomic criteri for distinguishing *E. canadensis* and *E. nuttallii* were no upheld in four of 20 populations sampled in western Mas sachusetts.

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LITERATURE CITED

ADAMS, F. S., D. R. MACKENZIE, H. COLE, JR., & M. W. PRICE 1971. The influence of nutrient pollution levels upon elemen constitution and morphology of *Elodea canadensis* Rich. i Michx. Environ. Pollut. **1**:285-298.

DARLINGTON, C. D. & E. K. JANAKI AMMAL. 1945. Chromosom atlas of cultivated plants. George Allen & Unwin, LTD, London, England.

ERNST-SCHWARZENBACH, M. 1945. Kreuzungsversuche an Hydro charitaceen. Arch. Julius Klaus-Stiftung **20**:22-41.

FASSETT, N. C. 1969. A manual of aquatic plants. The Universit of Wisconsin Press, Madison, Wis.

FERNALD, M. L. 1950. Gray's manual of botany. Eighth edition American Book Co., New York, N. Y.

GLEASON, H. A. 1952. The new Britton and Brown illustrate flora of the northeastern United States and adjacent Canada Lancaster Press Inc., Lancaster, Pa.

LIND, C. T., & G. COTTAM. 1969. The submerged aquatics of University Bay: a study in eutrophication. Am. Midl. Nat. 81 353-369.

LIVINGSTON, R. B. 1967. A guide to the spring and summer flora of western New England. Hamilton I. Newell Press, Amherst, Mass.

LIVINGSTON, R. B., & P. A. BENTLEY. Undated. The role of aquatic vascular plants in the eutrophication of selected lakes in Western Massachusetts. Publication No. 11. Water Resources Research Center, University of Massachusetts, Amherst, Mass.

MARIE-VICTORIN, FRERE. 1931. L'*Anacharis canadensis*, histoire et solution d'un imbroglio taxonomique. Contr. Lab. Bot. Univ. Montréal **18**:7-43.

MCCANN, J. A., & L. M. DALY. Undated. An inventory of the ponds, lakes, and reservoirs of Massachusetts. Berkshire and Franklin Counties. Publication No. 10-2. Water Resources Research Center, University of Massachusetts, Amherst, Mass.

MCCANN, J. A., & L. M. DALY. 1972. An inventory of the ponds, lakes, and reservoirs of Massachusetts. Hampden and Hampshire Counties. Publication No. 10-4. Water Resources Research Center, University of Massachusetts, Amherst, Mass.

MUENSCHER, W. C. 1944. Aquatic plants of the United States. Comstock Publishing Co., Inc., Ithaca, N. Y.

RADFORD, A. E., H. E. AHLES, & C. R. BELL. 1964. Manual of the vascular floras of the Carolinas. The University of North Carolina Press, Chapel Hill, N. C.

SANTOS, J. K. 1924. Determination of sex in *Elodea*. Bot. Gaz. **77**: 353-376.

SCULTHORPE, C. D. 1967. The biology of aquatic vascular plants. Edward Arnold, Publishers Ltd., London, England.

SEYMOUR, F. C. 1969. The flora of New England. The Charles E. Tuttle Company, Rutland, Vt.

SOKAL, R. R., & F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco, Cal.

ST. JOHN, H. 1965. Monograph of the genus *Elodea:* part 4 and summary. Rhodora **67**:1-35; 155-180.

STUCKEY, R. 1971. Changes of vascular aquatic flowering plants during 70 years in Put-in-Bay Harbor, Lake Erie, Ohio. Ohio J. Sci. **71**:321-342.

VOLKER, R., & S. G. SMITH. 1965. Changes in the aquatic vascular flora of Lake East Okoboji in historic times. Proc. Iowa Acad. Sci. **76**:65-72.

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ENUMERATION AND TYPIFICATION OF GENERA IN THE TRIBE CERCIDEAE[1]

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The tribe Cercideae (Leguminosae) was erected by Bronn (1822) and contained at that time the single genus *Cercis* L. Simultaneously Bronn erected the tribe Cassieae and placed in it 26 genera, including *Bauhinia* L. Subsequently Bentham (1840) erected the tribe Bauhinieae, placing it in *Bauhinia* L., *Casparia* Kunth, *Cercis* L., *Etaballia* Benth., and *Schnella* Raddi. The tribe Bauhinieae, with the inclusion of *Cercis*, is contribal with Cercideae. Until recently, most authors have used Bentham's tribal name, apparently unaware of Bronn's earlier name. Later Bentham (1865) reduced the number of genera to three: *Bauhinia*, *Cercis*, and a newly erected genus, *Bandeiraea* Welw. ex Benth. He transferred *Etaballia* to the tribe Dalbergieae and placed it in synonymy under *Inocarpus* Forst. In that treatment Bentham reduced *Schnella* to a section of *Bauhinia* and also recognized *Casparia* as a section of *Bauhinia* as was previously proposed by Candolle (1825). About the same time Baillon (1865) erected *Griffonia* which is considered congeneric with *Bandeiraea* by all later workers and antedates it by only eight days. The proximity of dates led to confusion regarding which name had priority, resulting in some authors accepting *Bandeiraea* over *Griffonia*.

In general, taxonomists have followed Bentham's second treatment of the tribe in recognizing three genera. Britton and Rose (1930) and Wit (1956) represent two outstanding exceptions to this. Britton and Rose recognized six genera in North America and erected *Caspareopsis*. Wit recognized seven genera in Malaysia, erected *Brac-*

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teolanthus, and elevated *Lysiphyllum* from sectional status within *Bauhinia* to generic level. Rafinesque (1838) had established the genera *Binaria, Cansenia, Elayuna, Mandarus, Monoteles,* and *Telestria,* in addition to recognizing *Casparia* and *Phanera,* all segregate genera of *Bauhinia;* Drake del Castillo (1902) first described *Gigasiphon;* Cuervo Marquez (1920) erected *Ariaria;* Rusby (1927) erected *Cardenasia;* and Torre and Hillcoat (1955) elevated *Adenolobus* and *Tylosema* from sectional status within *Bauhinia* to generic level. In addition to *Bauhinia, Cercis,* and *Griffonia,* several recent taxonomists also recognize *Gigasiphon* (e.g., Exell & Mendonca, 1956; Brenan, 1967; Aubreville, 1968), *Piliostigma* (e.g., Exell & Mendonca, 1956; Hutchinson & Dalziel, 1958; Brenan, 1967; Aubreville, 1968, 1970), *Tylosema* (e.g., Exell & Mendonca, 1956; Brenan, 1967), and *Adenolobus* (e.g., Exell & Mendonca, 1956) as distinct genera.

In view of the complex taxonomic history of the tribe and the time lapse since the last comprehensive evaluation (Taubert, 1892), a revision of the tribe seems to be in order. This paper constitutes the first step in such a proposed revision. It is intended to enumerate the validly published generic names which have been ascribed to the tribe and the typification of each. Five genera, *Cansenia* Raf., *Mandarus* Raf., *Siliquastrum* Tournef. ex Adans., *Telestria* Raf., and *Bauhinia* Raf., which were not previously typified, are lectotypified here in the interest of taxonomic stability. Orthographic variants and typographic errors are also listed under the appropriate generic names.

ADENOLOBUS (Harv.) Torre & Hillc. in Exell & Mend., Bol. Soc. Brot., ser. II **29**: 37. 1955. Based on *Bauhinia* sect. *Adenolobus* Harv. in Harv. & Sond., Fl. Cap. **2**: 275. 1862.

TYPE: *A. garipensis* (E. Mey.) Torre & Hillc. Based on *Bauhinia garipensis* E. Mey. Originally monotypic.

ALVESIA Welw., Apont. 587. 1858. *nom. rej.*
TYPE: *A. bauhinioides* Welw. Originally monotypic. The name antedates *Alvesia* Welw., 1869 [Labiatae], but the latter is a *nomen conservandum*.

AMARIA Mutis, Sem. Nuev. Gran. 2: 25. 1810.
LECTOTYPE: *A. petiolata* Mutis ex DC.
Two species were described by Mutis in the original publication with polynomials. Candolle (1825) validated these with binomials. The first of these two species has been designated as the lectotype by Britton and Killip (1936).

ARIARIA C. Marq., Estud. Arq. Etno. Amer. 1: 141. 1920.
TYPE: *A. superba* C. Marq. Originally monotypic.

BANDEIRAEA Welw. ex Benth. in Benth. & Hook. f., Gen. Pl. 1: 577. 1865 (ca. 19 Oct.). *Bandereia* Baill., Hist. Pl. 2: 210. 1870, typographic error.
LECTOTYPE: *B. simplicifolia* (Vahl ex DC.) Benth. ex Oliv. Based on *Schotia simplicifolia* Vahl ex DC. Bentham (1865) described the genus and noted that it contained two or three species including *Schotia simplicifolia*, but no transfers were made or new species described. Later Bentham (1866) described two new species and noted that one of them, *B. speciosa* Welw. ex Benth. was probably the same as *Schotia simplicifolia*. Five years later Oliver (1871) formally transferred *S. simplicifolia* into *Bandeiraea*. The person responsible for the designation of *B. simplicifolia* as the lectotype is not known to this investigator, but the species is generally accepted as the lectotype (*vide* Index Nominum Genericorum).

Bauhinia L., Sp. Pl. 374. 1753. *Bauhina* Corth., Disp. 22. 1790, orthographic error; *Bauhinea* Wats., Proc. Amer. Acad. Arts 25: 147. 1890, orthographic error.
LECTOTYPE: *B. divaricata* L. Eight species appeared in the original publication. Hitchcock and Green (1929) selected *B. divaricata* as the lectotype on the basis that the generic description was drawn by Linnaeus from that species.

BAUHINIA Kunth, Ann. Sci. Nat. (Paris) **1**: 85. 1824.
LECTOTYPE: *B. aculeata* L. Kunth's circumscription of *Bauhinia* excluded the type species of *Bauhinia* L., thereby creating a later homonym. Britton and Rose (1930) attempted to lectotypify *"Bauhinia* L." *sensu* Kunth with *B. aculeata* and effected a lectotypification of *Bauhinia* Kunth.

BAUHINIA Raf., Sylva Tellur. 121. 1838.
LECTOTYPE: *B. aculeata* L. In dividing *Bauhinia* L. into segregate genera, Rafinesque excluded the type species, thereby creating a second later homonym. Since no species were cited by Rafinesque, *B. aculeata* is here designated as the lectotype of *Bauhinia* Raf. which is the sense in which Rafinesque defined the genus.

BINARIA Raf., Sylva Tellur. 122. 1838.
TYPE: *B. cumanensis* (H.B.K.) Raf. Based on *Bauhinia cumanensis* H.B.K. Designated type in the original publication of the genus.

BRACTEOLANTHUS de Wit, Reinwardtia **3**: 415. 1956.
TYPE: *B. dipterus* (Bl. ex Miq.) de Wit. Based on *Bauhinia diptera* Bl. ex Miq. Originally monotypic.

CANSENIA Raf., Sylva Tellur. 122. 1838.
LECTOTYPE: *C. ungulata* (L.) Raf. Based on *Bauhinia ungulata* L. In the original publication of *Cansenia*, Rafinesque stated "Type *C.* or *B. angulata* and *tomentosa* ? st. monad." Since the basionym *B(auhinia) angulata* is a *nomen nudum*, it is excluded as a possible lectotype. Index Kewensis (**1**: 413. 1895) lists *Cansenia angulosa* and *Cansenia tomentosa* as being synonymous with *Bauhinia angulosa* and *Bauhinia tomentosa* respectively. Since the name *Bauhinia angulosa* was not validly published until 1939 by Vogel, and since Vogel's species does not fit the description of *Cansenia,* the citation of *C. angulosa* in Index Kewensis is undoubtedly an error. Whether the

question mark placed by Rafinesque in the statement of his protolog referred to the doubtful inclusion of *B. tomentosa* in *Cansenia* or to the stamen condition is debatable. However, *B. tomentosa* does not fit the description of *Cansenia* well and is therefore considered as an unsuitable choice for the lectotype. In the author's opinion, the specific epithet *angulata* is undoubtedly a typographical error for *ungulata*. *Bauhinia ungulata* does fit the description of *Cansenia*. Thus *Cansenia ungulata* (L.) Raf. is best chosen as the lectotype of *Cansenia*.

CARDENASIA Rusby, Mem. New York Bot. Gard. 7: 257. 1927.

TYPE: *C. setacea* Rusby. Originally monotypic.

CASPAREOPSIS Britt. & Rose, N. Amer. Fl. 23: 217. 1930.

TYPE: *C. monandra* (Kurz) Britt. & Rose. Based on *Bauhinia monandra* Kurz. Originally monotypic.

CASPARIA Kunth, Ann. Sci. Nat. (Paris) 1: 85. 1824 (? Jan.). *Casparea* H.B.K., Nov. Gen. Sp. 6: 317. 1824 (24 Apr.), orthographic error; *Cusparia* D. Dietr., Synops. 2: 1473. 1840, typographical error.

TYPE: *C. pes-caprae* (Cav.) H.B.K. Based on *Bauhinia pes-caprae* Cav. No combination was made by Kunth in the original publication of the genus, but in its subsequent republication as *Casparea* by Kunth in Humboldt and Bonpland, the single combination *C. pes-caprae* was made. Thus *Casparia* was originally monotypic.

CAULOTRETUS Rich. ex Schott in Spreng., L. Syst. Veg., ed. 16. 4(2): 406. 1827.

TYPE: *C. smilacinus* Schott. Originally monotypic.

CERCIS L., Sp. Pl. 374. 1753. *Circis* Chapm., Fl. S. U.S. 114. 1860, typographical error.

LECTOTYPE: *C. siliquastrum* L. The first of two species in the original publication was designated as the lectotype by Britton and Schafer (1908).

ELAYUNA Raf., Sylva Tellur. 145. 1838. *nom. rej.*

Type: *E. biloba* Raf., *nom. illeg.* New name for *Bauhinia tamarindacea* Del. Originally monotypic. The name antedates *Piliostigma* Hochst., 1846, but the latter is a *nomen conservandum.*

GIGASIPHON Drake del Cast. in Grandid., Hist. Phys. Madag. 30(1)88. 1902.

Type: *G. humblotianum* (Baill.) Drake del Cast. Based on *Bauhinia humblotiana* Baill. Originally monotypic.

GRIFFONIA Baill., Adansonia 6: 188. 1865 (7 Oct.).

Type: *G. physocarpa* Baill. Originally monotypic. *Griffonia* Baill. is also an earlier homonym of *Griffonia* Hook. f., 1865 (ca. 19 Oct.) [Rosaceae].

LACARA Spreng., Neue Entdeck. 3: 56. 1822.

Type: *L. triplinervia* Spreng. Originally monotypic. *Lacara* Spreng. is also an earlier homonym of *Lacara* Raf., 1836 [Campanulaceae].

LASIOBEMA (Korth.) Miq., Fl. Ind. Bat. 1: 71. 1855. Based on *Bauhinia* sect. *Lasiobema* Korth., Verh. nat. Gesch., Bot. 84. 1841.

Lectotype: *L. scandens* (L.) de Wit. Based on *Bauhinia scandens* L. Wit (1956) designated *L. scandens* (L.) de Wit as the lectotype which he considered the same as *L. anguina,* the only described species of three cited in the original publication of the section of *Bauhinia* by Korthals and the first of two cited in the original publication of the genus by Miquel.

LOCELLARIA Welw., Apont. 588. 1858.

Type: *L. bauhinioides* Welw. Originally monotypic.

LYSIPHYLLUM (Benth.) de Wit, Reinwardtia 3: 431. 1956. Based on *Bauhinia* sect. *Lysiphyllum* Benth. in Benth. & Hook. f., Gen. Pl. 1: 576. 1865.

Type: *L. cunninghamii* (Benth.) de Wit. Based on

Phanera cunninghamii Benth. Designated type in the original publication of the genus.

MANDARUS Raf., Sylva Tellur. 122. 1838.

LECTOTYPE: *M. divaricatus* (L.) Raf. Based on *Bauhinia divaricata* L. The first of four definitely, and one questionably, included species in the original publication is here designated as the lectotype. This genus was erected by Rafinesque to include the monandrous New World species of *Bauhinia* L. which is typified by *B. divaricata* L.

MONOTELES Raf., Sylva Tellur. 122. 1838.

TYPE: *M. paradoxa* Raf., *nom. illeg.* New name for *Bauhinia monandra* Kurz. Originally monotypic.

PAULETIA Cav., Icon. 5: 5. 1799.

LECTOTYPE: *P. inermis* Cav. The first of two species in the original publication has been designated as the lectotype by Wit (1956).

PERLEBIA Mart. in Spix & Mart., Reise Bras. 2: 555. 1828.

TYPE: *B. bauhinioides* Mart. Originally monotypic. *Perlebia* Mart. is also an earlier homonym of *Perlebia* DC., 1829 [Umbelliferae].

PHANERA Lour., Fl. Cochinch. 1: 37. 1790.

TYPE: *P. coccinea* Lour. Originally monotypic.

PILIOSTIGMA Hochst., Flora 29: 598. 1846. *nom. cons.* *Pileostigma* Benth. in Benth. & Hook. f., Gen. Pl. 1: 576. 1865, orthographic error.

LECTOTYPE: *P. reticulatum* (DC.) Hochst. Based on *Bauhinia reticulata* DC. The second and older of the two species cited in the original publication has been designated as the lectotype by Keay (1954). *Elayuna* Raf. antedates *Piliostigma,* but the latter is a *nomen conservandum.*

SCHNELLA Raddi, Mem. Soc. Ital. Modena 18: 411. 1820.

LECTOTYPE: *S. macrostachya* Raddi. The first of two spe-

cies cited in the original publication was designated by Britton and Rose (1930) as the lectotype.

SILIQUASTRUM Tournef. ex. Adans., Fam. **2:** 317. 1763.

LECTOTYPE: *S. arbor-judae* Medic., *nom. illeg.* New name for *Cercis siliquastrum* L. Adanson did not cite any species, thus the first of two species placed in the genus by Medicus (*in* Vorles, Churpf. Phys. Ges. **2:** 339. 1789) is here designated as the lectotype. The basis for this selection is that *S. arbor-judae* is a new name for *Cercis siliquastrum* L., the type species of *Cercis,* with which *Siliquastrum* is congeneric. *Siliquastrum* was proposed as a substitute name for *Cercis* on the basis that it was older, but it is pre-Linnean and can not be considered according to the rules of priority of the International Code of Botanical Nomenclature.

TELESTRIA Raf., Sylva Tellur. 122. 1838.

LECTOTYPE: *T. purpurea* (L.) Raf. Based on *Bauhinia purpurea* L. The first of two species cited in the original publication is here designated as the lectotype.

TOURNAYA Schmitz, Bull. Jard. Bot. Nat. Belg. **43:** 397. 1973.

TYPE: *T. gossweileri* (Baker f.) Schmitz. Based on *Bauhinia gossweileri* Baker f. Originally monotypic.

TYLOSEMA (Schweinf.) Torre & Hillc. in Exell & Mend., Bol. Soc. Brot., ser. II **29:** 38. 1955. Based on *Bauhinia* sect. *Tylosema* Schweinf., Reliq. Kotsch. 17. 1868.

TYPE: *T. fassoglensis* (Kotsch.) Torr. & Hillc. Based on *Bauhinia fassoglensis* Kotsch. Originally monotypic.

EXCLUDED GENERA

ETABALLIA Benth., Hook. Journ. Bot. **2:** 99. 1840.

TYPE: *E. guianensis* Benth. Two species were cited in the original publication. The first of these, *E. guianensis,* was given a latin diagnosis and probably served as the basis for

the generic description. The second was listed at the end of the discussion with only a short English diagnosis. It was later suppressed by Bentham (1842) as an error, thereby making *Etaballia* monotypic. The exact placement of this genus presently is in doubt, but it does not belong in the Cercideae (= Bauhinieae Benth.) as proposed by Bentham (*vide* Rudd, 1970).

PERLEBIA Schmitz, Bull. Jard. Bot. Nat. Belg. 43: 381. 1973, *nom. inval.*

The circumscription of *Perlebia* by Schmitz excluded the type species of *Perlebia* Mart. thereby creating a later homonym. However, Schmitz neglected to designate a type species for his *Perlebia* and thus his name is a *nomen invalidum* according to article 37 of the International Code of Botanical Nomenclature.

"SCHOTIARIA DC." Hutchinson, Gen. Fl. Pl. **1**: 241. 1964, error in citation.

Candolle (1825) described *Schotiaria* as a section of *Schotia* Jacq. containing the single species *Schotia simplicifolia* Vahl ex DC. This species is regarded as the type species of *Griffonia* Baill. The citation by Hutchinson of "*Schotiaria* DC. (1825)" as generic synonym of *Griffonia* is an error in citation and not a validly published generic name.

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LITERATURE CITED

AUBREVILLE, A. 1968. Legumineuses-caesalpinioidees in Flore du Gabon. No. 15. Paris. 362 p.

————. 1970. Legumineuses-caesalpinioidees in Flore du Cameroun. No. 9. Paris. 339 p.

BAILLON, H. 1865. Etudes sur l'herbier du Gabon. Adansonia **6**: 177-230.

BENTHAM, G. 1840. Contributions toward a flora of South America. — Enumeration of plants collected by Mr. Schomburgk in British Guiana. Hook. Journ. Bot. **2**: 38-103, 127-146, 210-223, 286-324.

————. 1842. *Etaballia guianensis*. Hook. Icon. Pl. 453-454.

————. 1865. *In* BENTHAM, G., and J. D. HOOKER. LVII. Leguminosae. Genera Plantarum. London. **1**: 434-600.

————. 1866. Description of some new genera and species of tropical Leguminosae. Trans. Linn. Soc. London **25**: 297-320.

BRENAN, J. P. M. 1967. Leguminosae subfamily Caesalpinioideae in Flora of Tropical East Africa. London/Tonbridge. 230 p.

BRITTON, N. L., & E. P. KILLIP. 1936. Mimosaceae and Caesalpiniaceae of Colombia. Ann. New York Acad. Sci. **35**: 101-208.

————., & J. N. ROSE. 1930. Caesalpiniaceae. N. Amer. Fl. **23**: 201-349.

————., & J. A. SCHAFER. 1908. North American Trees. New York. 894 p.

BRONN, H. G. 1822. De Formis Plantarum Leguminosarum Primitivis et Derivatis. Heidelberg. 140 p.

CANDOLLE, A. P. DE. 1825. Prodromus Systematis Naturalis Regni Vegetabalis: Leguminosae. Paris. **2**: 93-524.

CUERVO MARQUEZ, C. 1920. El Llano. Part IX: El Ariari, *in* Estudios Arqueologicos y Etnograficos Americanos. 2ª ed. corr. y aun. **1**: 99-143. Edit. America/Madrid [not seen].

DRAKE DEL CASTILLO, E. 1902. Histoire Naturelle des Plantes, *in* A. Grandidier. Histoire, Physique, Naturelle et Politique de Madagascar. Paris **30(1)**: 1-208.

EXELL, A. W., & F. A. MENDONCA. 1956. *In* CARRISSO, L. W. Leguminosae (Caesalpinioideae-Mimosoideae). Conspectus Florae Angolensis. Lisboa. **2**: 162-299.

HITCHCOCK, A. S. & M. L. GREEN. 1929. Standard-species of Linnaean Genera of Phanerogams (1753-54), pp. 111-199. *In* International Botanical Congress, Cambridge, England, 1930. Nomenclature. Proposals by British Botanists. London.

HUTCHINSON, J., & J. M. DALZIEL. 1958. Caesalpinioideae in Flora of West Tropical Africa. 2nd ed., revised by R. W. J. Keay. London/Tonbridge. **1(2)**: 439-484.

KEAY, R. 1954. Proposal for the conservation of the generic nam *Piliostigma* (Leguminosae). Proposal no. 159. Taxon **3**: 65-6
OLIVER, D. 1871. Caesalpinieae in Flora of Tropical Africa. Ash ford. **2**: 258-321.
RAFINESQUE, C. S. 1838. Sylva Telluriana. Philadelphia. 184 p.
RUDD, V. E. 1970. *Etaballia dubia* (Leguminosae), a new com bination. Phytologia **20**: 426-428.
RUSBY, H. H. 1927. Descriptions of new genera and species o plants collected on the Mulford Biological Exploration of th Amazon Valley. Mem. New York Botanical Gard. **7**: 205-28
TAUBERT, P. 1892. *In* ENGLER, A., & K. PRANTL. Caesalpinioidea — Bauhinieae (*in* Leguminosae). Die naturlichen Pflanzenfam ilien. Leipzig. **3**^{3} **(71)**: 146-153.
TORRE, A. R., & D. HILLCOAT. 1955. *In* EXELL, A. W., & F. A MENDONCA. Novidades da flora de Angola IV. Bol. Soc. Bro ser. II. **29**: 29-44.
WIT, H. C. D. DE. 1956. A revision of Malaysian Bauhinieae. Rei wardtia **3**: 381-541.

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SOUTH AMERICAN LINUM, A SUMMARY

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Linum is a genus of perhaps 150 species, widely distributed throughout the temperate and subtropical regions of the world. The greatest number and diversity of species are in the eastern Mediterranean region, where all of the usually recognized sections of the genus are represented. Studies of the North American flaxes (Rogers, 1963, 1968, 1969) have shown that they are related to and probably had their origin among Old World plants. It has seemed worthwhile to learn more about the relationships of the several South American species. The present paper, for which much of the information comes from the dissertation of Mildner (1971), summarizes the results of this study. With the aid of a Sigma Xi Grant-in-Aid of Research to the senior author it has been possible for both of us to observe most of the species in the field and to collect various kinds of materials. Herbarium specimens have been borrowed from a number of institutions and the help of the several curators is gratefully acknowledged. For certain South American species the reexamination of specimens housed in Old World herbaria will be needed before their final circumscription and typification can be determined and synonymy finalized. When these questions have been resolved, a revision of the genus in South America, including detailed descriptions of the species, can be presented, but there are enough data now available to summarize many of the relationships of the South American plants to each other and to species in other parts of the world.

Although *Linum bienne* Huds., *L. usitatissimum* L. and perhaps, occasionally, other Old World species may be found as adventives or escapes from cultivation, the native South American species are confined to two sections of the genus, *Cliococca* and *Linastrum*. The former monotypic section differs so greatly from the rest of the genus that

it is much better treated as a separate genus (Rogers & Mildner, 1972). *Linastrum* is probably the largest and most widespread section of the genus, being found not only in several parts of the Old World, but including all but two or three of the approximately forty native North American species.

There may be as many as seventeen or eighteen taxa in South America. Their total known distribution (together with the presumed direction of increased specialization) is shown in Figure 1. As can be seen, although there are minor centers of diversity in Peru and Chile, the principal concentration of *Linum* species is along the eastern side of the continent, from southeastern Brazil near Rio de Janeiro southward through Uruguay to northeastern Argentina. Two or three species are of special interest. The Brazilian plants, *L. organense* Gardn. and especially *L. smithii* Mildner, are broad-leaved plants which are very similar to the North American *L. schiedeanum* Schlecht. & Cham. (Mexico-Texas) and *L. nelsonii* Rose (Mexico-Nicaragua), as well as to several species of South Africa, such as *L. quadrifolium* L. The narrow-leaved *L. burkartii* Mildner, of Uruguay and northeastern Argentina, is also very similar to African plants such as *L. holstii* Engelm. and almost identical to the North American *L. rupestre* (A. Gray) Engelm. (Mexico-Texas). The North American species mentioned, on the basis of the comparative study of a series of characters, are believed to possess the greatest number of primitive features of any of the North American species (Rogers, 1969). Their similarity to the South African plants was also noted.

The general distribution and morphology of the whole genus and of the section *Linastrum* suggest that the transatlantic migration which accounts for these disjunct, closely related plants most likely was from the Old to the New World. Whether, in this event, the establishment of *Linum* in South America was independent of that in North America or whether the genus became established in one area in the New World and then spread to the other would

be quite conjectural. On the basis of the amount of diversification which has taken place on the two continents, if this may be used as a possible measure of the time available for evolution, it is quite clear that the amount of change that has taken place on the North American continent far exceeds that in South America. As many as thirty-five to forty species have evolved in North America, including some, such as *L. rigidum* Pursh, which are among the most highly specialized in the whole genus. Moreover, there is evidence that the genus *Hesperolinon* (and probably *Sclerolinon*) of the western United States has also evolved from North American species of the section *Linastrum* (Rogers, 1975). On the other hand, while *L. smithii, L. organense* and *L. burkartii* are distinctive, the South American flaxes in general are a very closely allied group of species. The following discussion will illustrate this.

The "*Linum littorale* St. Hil. complex" which ranges from east-central Brazil to Uruguay, is a troublesome one, the source of a number of named forms, varieties and species. These are described in some detail in the Flora Ilustrada Catarinensis (Rogers & Smith, 1975) wherein *L. palustre* Gardn., a slender plant with much reduced terminal inflorescences, *L. brevifolium* St. Hil. & Naud, with racemose inflorescences, and *L. littorale,* with open inflorescences, are recognized. *Linum carneum* St. Hil. and *L. erigeroides* St. Hil., described in the same publication, are two very closely related species, characterized by thicker-textured sepals and more obtuse fruits than *L. littorale*. They range from southern Brazil to eastern Argentina. Some collections of *L. littorale,* in the southern part of its range, seem to intergrade with one or another of them. *Linum carneum* and *L. erigeroides* in turn differ only slightly from *L. scoparium* Griseb., a bushy branched species ranging from eastern Uruguay to central Argentina and northward to the Bolivian-Peruvian border near La Paz. Although there is a small geographical separation, *L. scoparium* in that area closely resembles collections of

Peruvian plants usually called *L. oligophyllum* Willd. (the identity of the type with this population needs further verification). In northern Peru and Ecuador an admixture of closely allied populations, differing only slightly from *L. oligophyllum*, have been called *L. filiforme* Urb., while in sandy coastal areas from the vicinity of Lima, Peru, to northern Chile (Paposo), small-flowered plants, also not too different from *L. oligophyllum*, are interpreted as *L. prostratum* Domb. ex Lam. (the type specimen may need verification).

Of most interest in terms of the general picture of relationships among the flaxes of western South America is the sequence of minor variations, including trends toward larger floral parts and more nearly united styles, leading from *Linum oligophyllum*, with separate styles and petals about ten mm. long, to the generally much stouter *L. macraei* Benth. of central Chile, with styles united nearly to the summit and petals up to 20 mm. long. Several of the intermediates have been named, of which *L. polygaloides* Planch., of southwestern Peru, and *L. ramosissimum* Gay, of the Fray Jorge region of central Chile, may be the most substantial. Well-defined species in Chile are the procumbent, mat-forming, highly localized *L. cremnophilum* Johnst., near Taltal, and the separate-styled *L. chamissonis* Schiede in the Concepción area.

In summary it may be said that the flaxes which grow along the eastern part of the South American continent, from southeastern Brazil southward to northeastern Argentina, display the greatest array of variation and include some species which very closely resemble plants of North America and southern Africa. There is an almost continuous series of populations extending from northeastern Argentina generally northward through western Bolivia and adjacent Peru, across the Andes in Peru and thence southward along the Pacific Coast to central Chile. The species of Brazil, Uruguay and Argentina are thought to include the least specialized of the genus on the continent in terms of their possession of characteristics found in species in

other parts of the world. The plants of Chile, particularly *Linum cremnophilum* and *L. macraei* must be considered the most highly specialized of the genus in South America. These general relationships are summarized in Figure 1.

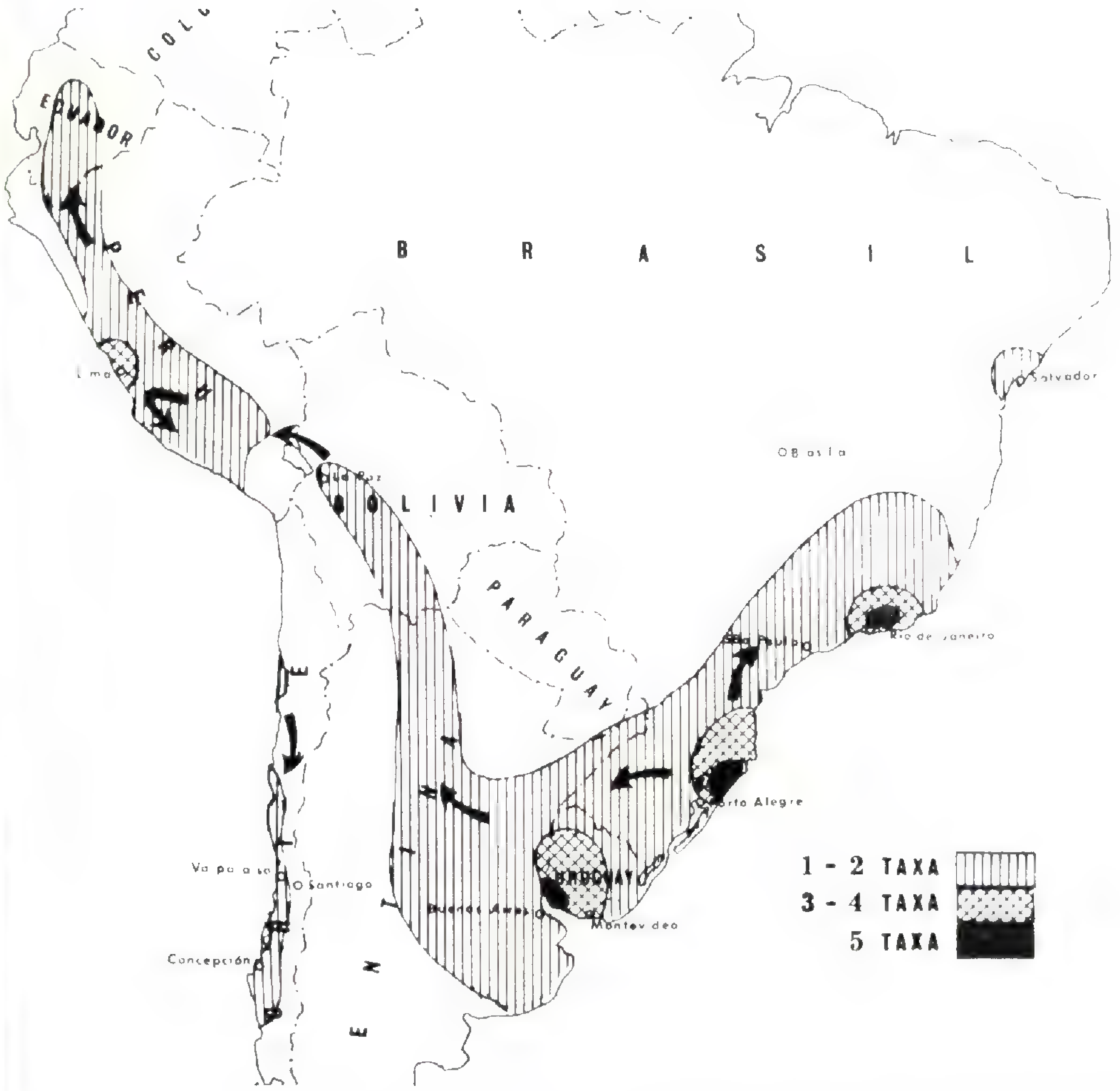

Figure 1. Distribution of *Linum* in South America, showing the direction of presumed increase in specialization.

LITERATURE CITED

MILDNER, R. A. 1971. Systematic Studies in South America *Linum* (flax). Ph.D. Dissertation, Wayne State University Detroit, Mich.

ROGERS, C. M. 1963. Yellow-flowered species of *Linum* in easter North America. Brittonia **15**: 97-122.

————. 1968. Yellow-flowered species of *Linum* in Centra America and western North America. Brittonia **20**: 107-135

————. 1969. Relationships of the North American Species o *Linum* (Flax). Bull. Torr. Bot. Club **96**: 176-190.

————. 1975. The Relationships of *Hesperolinon* and *Linum* (Linaceae). Madroño **23**: 153-159.

————., and R. A. MILDNER. 1971. The Reevaluation of the Genus *Cliococca* (Linaceae) of South America. Rhodora **73** 560-565.

————., and L. B. SMITH. 1975. Lináceas in Flora Ilustrada Catarinense.

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THE SPREAD OF SEVERAL INTRODUCED OR RECENTLY INVADING AQUATICS IN WESTERN MASSACHUSETTS

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In the course of a larger study of the vegetation of marshes of the Connecticut River watershed in western Massachusetts, changes in the distributional status of several introduced or invading aquatic vascular plant species have been observed. Each of these species was first collected in the area within the present century and has recently increased in sites affected by eutrophication or other habitat disruption; none is yet so widespread that it is regularly encountered in freshwater systems.

The spread of water clover, *Marsilea quadrifolia* L. from Paradise Pond on the Smith College campus in Northampton downstream two miles in disturbed sites along the Mill River during the period 1945-65 has been documented previously (Burk, 1966). Prior to 1969, *M. quadrifolia* failed to establish itself in the Arcadia Wildlife Sanctuary marsh at the mouth of the river, although at least one small colony persisted there for portions of a single season. During summer, 1969, at a time when the Arcadia marsh was severely disturbed by upstream industrial pollution, an oil spill, a dredging operation, and seepage from a municipal dump, *M. quadrifolia* became established over several hundred square feet of exposed substratum near the outlet of the Mill River into the oxbow of the Connecticut. This colony expanded and by early fall of 1970, *M. quadrifolia* was generally distributed and abundant in the marsh (Robinton and Burk, 1971) where it has competed successfully with native vegetation to the present despite a general improvement of water quality within the stream. As of September, 1974, *M. quadrifolia* had not spread into the oxbow of the Connecticut. Colonies of *M. quadrifolia* have maintained themselves along the river between Ar-

cadia marsh and Paradise Pond but have not extended farther upstream than their farthest station, about 1550 feet from the assumed point of release, in 1965.

Wolffia columbiana Karst. was first collected in Massachusetts in 1933 by Manning (1934) in a small marsh at Mt. Tom Station, Holyoke. Eaton (1939) reported *W. columbiana* as abundant in the Great Meadows at Concord in 1938 in water largely derived from municipal filter beds. A third Massachusetts station was reported in 1951 by Harris and Bean at Methuen, Essex Co., while Eaton in 1952, 1957, and 1958 described its increased abundance correlated with increased pollution by alkaline sewage. Livingstone (1967) cites *W. columbiana* as rare in an area encompassing Franklin, Hampshire, and Hampden counties in western Massachusetts except at Leverett Pond, Hampshire Co., where a specimen (MASS 26585) documents its presence as early as 1953. Recently *W. columbiana* has become very abundant at a number of Hampshire County sites including Lake Warner in North Hadley, Aldrich Lake and Forge Pond, Granby, and South Pond in Hatfield. We have observed the Lake Warner site regularly since 1971; *W. columbiana* has persisted on the surface throughout the entire year, reaching densities, in mixed colonies with *Lemna minor* and *Spirodela polyrhiza*, sufficient to cover much of the zone of open water. Lake Warner, Aldrich Lake, and Forge Pond all receive sewage effluents and have been shown to be highly eutrophic compared with other western Massachusetts lakes (Snow and DiGiano, 1973); the increase in *W. columbiana* within this portion of its range thus seems almost certainly correlated with increased enrichment.

The water chestnut, *Trapa natans* L., became well established in eastern Massachusetts during the latter portion of the 19th century, reaching nuisance proportions by 1899 (Cook, 1899) and undergoing a striking increase along the Sudbury River in the 1940's (Eaton, 1947). This later increase was apparently associated with increased levels of soluble nitrates in the stream. The Mount Holyoke College

herbarium contains a fruiting specimen of *T. natans* (*A. M. Starr,* September, 1920) from Upper Lake on the Mount Holyoke Campus in South Hadley and Livingstone (1967) describes *T. natans* as rarely established in ponds within the region. At present, *T. natans* is abundant on Upper and Lower Ponds where herbicides have been used on occasion to control it. Both Upper and Lower Ponds are impoundments of Stony Brook; a search downstream in August, 1974, yielded a well established colony of *T. natans* covering several hundred square feet of water surface behind a dam at an abandoned paper mill near the intersection of Stony Brook with Route 116.

R. B. Livingstone (personal communication) has described a bizarre situation in which *Trapa natans* from the South Hadley population, and *Marsilea quadrifolia* and *Azolla caroliniana* Willd. from the Botanical Gardens of Smith College were deliberately introduced into a pond on the campus of the University of Massachusetts in Amherst in the early 1950's. All three species multiplied at such a rate that the pond was drained in an attempt to eliminate them. *Trapa natans* and *Azolla caroliniana* disappeared after a few years; *Marsilea quadrifolia* remained at pest densities through the middle 1960's but has since declined concomitant with increased turbidity within the pond caused by adjacent construction work. *Azolla caroliniana* has been introduced into various ponds in the Northampton area, both deliberately or through accident, yearly at least since 1966. It frequently multiplies to the extent of covering the entire water surface within a period of a few months but has not as yet survived the winter.

Cabomba caroliniana Gray was first reported from Massachusetts by Manning (1937) who found the species very abundant in South Pond, an ancient oxbow of the Connecticut River in Hatfield, Hampshire Co. Manning quoted a local florist as having observed *C. caroliniana* in abundance there for at least ten years; Manning's first collection of *C. caroliniana* at the site was made in 1930. Gates (1958) documents the extent of its occurrence in the state through

the 1950's; the South Pond station was the only collection west of Worcester Co. Hodgdon (1959) noted its spread at pest densities in Rockingham Co., New Hampshire.

The South Pond population has maintained itself to the present, *Cabomba caroliniana* comprising a major proportion of the submergent vegetation in the pond but not spreading downstream in Cowbridge Brook, which drains the oxbow into the Connecticut. Flowering and fruiting do not occur regularly on an annual basis in South Pond. In September, 1972, numerous specimens of *C. caroliniana* were observed there in flower or fruit, while during an extensive 1974 study of the vegetation of the pond, no flowering whatever was observed. In Lake Rohunta in Worcester and Franklin Counties a population which has persisted at least since 1963, as evidenced by specimens in the herbarium of the University of Massachusetts (MASS 47419, 47421), was observed flowering in October, 1974. *Cabomba caroliniana* is the dominant submerged aquatic throughout much of Lake Rohunta; is now occurs also in nearby South Athol Pond and has spread from Lake Rohunta from drainage into a tributary of the Millers River. We have also collected *C. caroliniana* with *Trapa natans* at its lowermost site on Stony Brook in South Hadley. *Cabomba caroliniana*, the origin of which is presumably more southerly areas, remains in actively growing condition later than other submerged aquatics, including *Ceratophyllum demersum* L. and various species of *Potamogeton*. Indeed, we observed and later collected bright green shoots of *C. caroliniana* in water under a layer of ice in Lake Rohunta in late January, 1975.

Miscanthus sacchariflorus (Maxim.) Hackel has been reported from two New England stations, one of which is in eastern Massachusetts (Seymour, 1969). We have found this grass, a native of China and Japan, well established around the edges of a small pond bordering the eastern side of Route 116 in South Hadley, Hampshire County.

Specimens of all species mentioned in this paper have been deposited in the Smith College herbarium. Nomen-

clature follows Fernald (1950) except in the instance of *Miscanthus sacchariflorus*, which he does not include.

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LITERATURE CITED

BURK, C. J. 1966. *Marsilea quadrifolia* in western Massachusetts. Am. Fern Jour. **53**: 140-141.

COOK, M. P. 1899. Some additions to the flora of Middlesex County, Massachusetts. Rhodora **1**: 80-82.

EATON, R. J. 1939. *Wolffia columbiana* in Concord, Massachusetts. Rhodora **41**: 41-42.

————. 1947. *Lemna minor* as an aggressive weed in the Sudbury River. Rhodora **49**: 165-173.

————. 1952. Status of *Phragmites communis* var. *Berlandieri* along the Sudbury River in eastern Massachusetts. Rhodora **54**: 135-137.

————. 1957. *Echinochloa walteri* in Concord, Massachusetts. Rhodora **59**: 264-265.

————. 1958. Some interesting records from eastern Massachusetts. Rhodora **60**: 316-320.

FERNALD, M. L. 1950. Gray's Manual of Botany. 8th ed. American Book Co. New York.

GATES, B. N. 1958. *Cabomba caroliniana* grows in Worcester County, Massachusetts. Rhodora **60**: 321-323.

HARRIS, S. K. & R. C. BEAN. 1951. *Wolffia columbiana* in Methuen, Massachusetts. Rhodora **53**: 272.

HODGDON, A. R. 1959. *Cabomba caroliniana* in Rockingham County, New Hampshire. Rhodora **61**: 248-249.

LIVINGSTONE, R. B. 1967. A Guide to the Spring and Summer Flora of Western New England. Newell Press, Amherst, Massachusetts.

MANNING, W. C. 1934. *Wolffia* in Massachusetts. Rhodora **36**: 240.

————. 1937. New records for the Connecticut Valley in Massachusetts. Rhodora **39**: 186-188.

ROBINTON, E. D., & C. J. BURK. 1971. The Mill River and its Floodplain in Northampton and Williamsburg, Massachusetts: A study of the Vascular Flora, Vegetation and the Presence of the Bacterial Family Pseudomonadaceae in Relation to Patterns of Land Use. Water Resources Research Center, U. of Mass. at Amherst. 72 pp.
SEYMOUR, F. C. 1969. The Flora of New England. Charles E. Tuttle Company, Inc., Tokyo, Japan.
SNOW, P. I., & F. A. DI GIANO. 1973. Relationships Between Trophic State and Chemical Parameters In Sediment-Water Systems of Selected Massachusetts Lakes. Division of Water Pollution Control. Mass. Water Resources Commission, Contract Number 15-51452. U. of Mass. at Amherst. 91 pp.

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A NEW VERONICA (SCROPHULARIACEAE) HYBRID FROM NEBRASKA

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Recent field and herbarium studies have led to the discovery of a naturally occurring putative hybrid in the genus *Veronica* L. (Scrophulariaceae) from Nebraska. Spontaneous interspecific hybrids in the Scrophulariaceae are infrequent, and to my knowledge, no hybrids within *Veronica* have been previously reported. The putative parents of this hybrid are *V. anagallis-aquatica* L. and *V. catenata* Pennell.

Three unusual specimens were found in the University of Kansas herbarium and another specimen was located in the University of Nebraska-Lincoln herbarium. All collections were made in the Platte River valley of central and western Nebraska. Following the treatment of Pennell (1921), I determined that these plants were morphologically intermediate between *V. anagallis-aquatica* and *V. catenata.*

In August, 1974, I collected one to three hybrid plants from three wet, sandy riverbank sites along the Platte and North Platte Rivers in Nebraska. At each location I also made collections of the presumed parental species, *V. anagallis-aquatica* and *V. catenata. Veronica anagallis-aquatica* was more abundant in all these areas.

Some characteristics of the hybrid and its putative parents are listed in Table 1. Determination of young hybrids is difficult because most characters of the hybrids are intermediate between those of the parental species. Mature hybrids are readily distinguished from *V. anagallis-aquatica* and *V. catenata* primarily by the shriveled calyxes that result when an expanded seed-bearing capsule does not form. The result is a long raceme composed of many

[1]I wish to acknowledge funds received from the Bridwell Foundation, Wichita Falls, Texas, which made this research possible.

short, contracted calyxes on long, slightly ascending pedicels. Both parental species produce expanded capsules when seed is set, giving the inflorescence a heavier, thicker appearance than in the hybrid plants.

As an indication of pollen viability, pollen stainability tests were made on the hybrid plants and their putative parents. Fresh pollen samples were stained with aniline blue in lactophenol; fully formed pollen grains with evenly staining cytoplasm were considered viable. Pollen grains from the hybrid plants were contracted, malformed, and less than 5% stainable. In contrast, the grains of *V. anagallis-aquatica* and *V. catenata* were fully formed and always more than 85% stainable.

The fact that few interspecific hybrids were found, even after extensive field work, indicates that well-developed mechanisms preventing hybridization between *V. anagallis-aquatica* and *V. catenata* exist. Laboratory investigations are in progress to determine the breeding system and cytogenetics of the proposed hybrid and its parents. In view of my findings at this time I present the following:

Veronica anagallis-aquatica × *catenata.*

Plants decumbent to erect, 3-7 dm tall; leaves sessile, 2-4 times as long as broad, entire to crenate-serrate; racemes 20-50-flowered; pedicels slightly ascending, longer than the perianth; calyx 1.0-1.8 mm broad near base; style 1.6-1.8 mm long; capsules shriveled or absent; pollen grains aborted.

SPECIMENS EXAMINED: **Nebraska:** DAWSON CO.: southeast of Gothenburg in Platte River bed, *Morrison* 1056 (NEB). GARDEN CO.: 1 mi. s. & 0.5 mi. e. Lewellen, low wet prairie, *Bare & McGregor* 1432 (KANU). KEITH CO.: 1 mi. s. Lemoyne, wet sandy shore of Lake McConaughy, *Brooks* 8008 (KANU). MERRICK CO.: 0.5 mi. w. Merrick-Polk Co. line on N-92, oxbow of Platte River, sandy, *Magrath* 6048 (KANU). MORRILL CO.: Bridgeport State Recreation Area, sandy margin of lake, *Richardson & Robinson* 1639 (KANU). POLK CO.: 11 mi. n. Osceola, sandy wet brushy bank of Platte River, *Brooks* 7816 (KANU).

LITERATURE CITED

Pennell, F. W. 1921. *Veronica* in North and South America. Rhodora 23:1-22, 29-41.

Table 1. Characteristics of *Veronica anagallis-aquatica* × *catenata* and its putative parents.

	V. anagallis-aquatica	Hybrid	*V. catenata*
1. Habitat	low wet sandy meadows and stream banks, common	wet sandy stream banks, rare	low wet sandy meadows and stream banks, scattered
2. Plant Height	2-8 dm	3-7 dm	1-3 dm
3. Leaves	1.5-3 times as long as broad	2-4 times as long as broad	3-5 times as long as broad
4. Racemes	30-60-flowered	20-50-flowered	15-30-flowered
5. Pedicels	4-8 mm long, ascending	3.5-5 mm long, slightly ascending	3-6 mm long, divaricately spreading
6. Calyx	expanded	shriveled and contracted	expanded
7. Capsules	present, expanded, 2.4-4.3 mm broad	absent or reduced and shriveled, 0.5-1 mm broad	present, expanded, 2.3-3.5 mm broad
8. Seed-set	present	absent	present
9. Style	1.5-2 mm long	1.6-1.8 mm long	1.2-1.7 mm long
10. Pollen	normal, >85% stainable	aborted, <5% stainable	normal, >90% stainable

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THE HOYSRADT HERBARIUM

Robert R. Smith

In the late 1860's a self-taught botanist, Lyman H. Hoysradt, started a personal herbarium to which he would soon be adding exchange specimens from many North American plant collectors. The collection included flowering plants, ferns and fern allies from the North American continent with few specimens from Trinidad and other parts of the world.

Lyman Henry Hoysradt, the first child of Cornelius and Catherine Lasher Hoysradt, was born December 11, 1848, in the old Hoysradt homestead on Stissing Lake. This lake is near Pine Plains, Dutchess County, New York state. Upon the death of his father, which occurred sixteen years later, the family moved to Pine Plains. Hoysradt's own formal education ended with the eighth grade, but through his interest in the sciences and his drive to become educated, he mastered the higher mathematics of his day and the science disciplines. His first love, however, was botany. He was most active in herbarium work between the ages of twenty-two and thirty-five. During this time span he was a teacher of mathematics and natural science at the Seymour Smith Academy in Pine Plains. It was also during this time span that Hoysradt did his most intensive collecting and exchanging of plant specimens. As a result of his efforts, he acquired a herbarium of over 20,000 specimens. He also wrote four articles which appear in the Bulletin of the Torrey Botanical Club. Hoysradt (Fig. 1) made his mark and contribution along with many others to botanical studies in the 1800's.

Hoysradt's field activities and drive to continue the herbarium efforts waned when he went to New York City to work in the United States Customs House. He stayed there for four years, and then returned to teaching. His

Lyman Henry Hoysradt (1848-1933) about age 35. This photo-
aph was taken at the time Mr. Hoysradt was most active in his
tanical studies and in the development of his personal herbarium.
hoto by Vail Bros., Poughkeepsie, N.Y., ca. 1883.

new position was in the Old Grove Street School in Ne York City, where he remained until his retirement.

Upon his retirement Hoysradt moved back to Pin Plains, and revived his botanical interests in the directio of horticulture. His specialty was working with peonie This hobby soon became somewhat of a small family bus ness, which lasted until his death, Aug. 6, 1933.

During his active years of acquiring a herbarium Hoysradt collected thousands of specimens. His excellen personal collection was from the Pine Plains area, Catski Mountains, the New Jersey Pine Barrens, and variou locations in New England. Many of the persons with whor he exchanged specimens are listed in the Botanical Direc tory for America — 1878.

After Hoysradt's death the family retained the her barium for ten years. It was then given by Mrs. L. H Hoysradt to Hartwick College, where it was stored fo over fifteen years.

In the late 1950's, Dr. Rogers McVaugh, eminent plan taxonomist, traced the Hoysradt collection to Hartwic College. Through McVaugh's recognition of the value o the herbarium, Dr. F. W. Miller, chairman of the biolog department at Hartwick College at the time, applied fo and obtained a National Science Foundation grant t organize the herbarium. This grant was utilized in th summer of 1958 by Dr. Mildred Faust, then of Syracus University, who completed an initial organization of th collection. At the present time the Hoysradt Herbarium i situated in Miller Science Hall of Hartwick College, an it is being further organized and made available for studie and loans.

Not only does the herbarium contain a fine collection o plants of the Pine Plains, N.Y. area, but it also contain many unique exchange specimens: for example, *Asplenium bradleyi* D. C. Eaton collected by Bradley and Eaton at th type locality, and *Cheilanthes parryi* (D. C. Eaton) Domin collected by C. Parry.

LIST OF PUBLICATIONS BY L. H. HOYSRADT

Solea concolor Ging. Bull. Torrey Bot. Club 5: 37, 38. (Sept.) 1874.

Flora of Pine Plains, Dutchess Co., N.Y. Bull. Torrey Bot. Club 5: 46-48. (Nov.) 1874.

Valeriana sylvatica Rich. Bull. Torrey Bot. Club 6: 53. (Sept.) 1875.

Catalogue of the Phaeogamous (sic) and Acrogenous Plants Growing without Cultivation within Five Miles of Pine Plains, Duchess (sic) Co., N.Y. Bull. Torrey Bot. Club 6: supplement 32 pp. 1875-79.

LIST OF COLLECTORS WITH WHOM HOYSRADT EXCHANGED SPECIMENS WITH GENERAL LOCATION OF EXCHANGE SPECIMENS IN THE HERBARIUM

Adams, C. F. (Florida); Allen, J. A. (Maine); Allen, Dr. T. F. (New York); Allmendinger, E. C. (Michigan); Anderson, Dr. C. L. (California); Arnold, C. N. (New York); Arthur, J. C. (Iowa); Austin, C. F. (Florida); Austin, Mrs. R. M. (California).

Babcock, H. H. (Illinois); Bagg, Mrs. S. C. (Arizona, California); Bailey, W. W. (Rhode Island); Barnes, C. R. (Indiana, Kentucky); Barnes, K. S. (New York); Barnstead, Dr. (New Hampshire); Bebb, M. S. (Illinois); Berger, J. G. (Illinois); Bishop, E. F. (Massachusetts); Blake, Rev. J. (Maine, New Hampshire); Bolander, H. N. (California); Boott, W. (Maine, Massachusetts, Michigan, New Hampshire, New York); Bradley, F. H. (Kentucky, Tennessee); Brainerd, E. (Massachusetts, Vermont); Brandegee, T. S. (Colorado, New Mexico); Brendel, Dr. F. (Illinois); Brooks, Dr. E. (California); Burgess, Rev. R. (Iowa); Bury, R. (Oregon); Bushnick, E. (Florida); Bustwick, H. (New York); Bustwick, I. (New York); Butler, G. D. (Indian Territory, Oklahoma).

Canby, W. M. (Delaware, New Jersey, North Carolina); Chickering, J. W., Jr. (Maryland, New Hampshire, New Jersey, New York, North Carolina, Virginia); Clark, Dr. I (Michigan); Cleveland, D. (California); Clinton, Judge G. W. (New York); Commons, A. (Delaware, New Jersey); Congdon, J. W. (Massachusetts, New Hampshire, Rhode Island, Vermont); Cooper, Mrs. S. P. (California); Coulter, J. M. (Indiana); Curtiss, A. H. (Florida, Georgia, North Carolina, South Carolina, Tennessee, Virginia); Curtiss, Mrs. F. A. (Florida).

Davenport, G. (Massachusetts); Diffenbaugh, G. (New Jersey); Dooley, J. (Massachusetts, New York).

Eaton, D. C. (Kentucky); Edwards, W. (California).

Faxon, C. E. (Massachusetts); Fendler, A. (Trinidad); Ferguson, E. D. (California); Flint, W. F. (New Hampshire); Fowler, Rev. J. (New Brunswick); French, G. H. (Illinois); Frost, C. C. (Vermont).

Garber, Dr. A. P. (Florida, Pennsylvania); Gattinger, Dr. A. (Tennessee); Gerard, W. R. (New York); Gray, Dr. A. (North Carolina); Gregor, F. (Wisconsin); Griffith, J. P. C. (Pennsylvania); Guttenberg, G. (West Virginia).

Hall, E. (Illinois, Texas); Harlow, Mrs. F. J. (Tennessee); Harrison, W. H. (New Jersey, Pennsylvania); Harvey, F. L. (Arkansas, Texas); Horsford, F. V. (Vermont); Howell, J. (Oregon); Howell, T. J. (Oregon, Washington); Hunt, E. (Massachusetts, New York); Hussey, J. (Kentucky); Hyams, M. E. (North Carolina).

James, J. F. (Ohio); Jesup, Rev. H. G. (Connecticut, Massachusetts, New Hampshire, Vermont); Jones, L (British Columbia); Jones, M. E. (Iowa, Utah); Joor, Dr. J. F. (Illinois).

Kellerman, W. A. (Wisconsin); Knipe, Rev. S. W (Pennsylvania).

Lemmon, J. G. (Arizona, California, Nevada).

Macoun, J. (Alberta, British Columbia, Manitoba, New Brunswick, Ontario, Quebec, Saskatchewan); Martindale,

I. C. (New Jersey, Pennsylvania); Mead, Dr. S. B. (Illinois); Mertz, H. N. (West Virginia); Miller, E. S. (New York); Miller, F. A. (California); Morong, Rev. T. (District of Columbia, Massachusetts, New Hampshire, New Jersey, New York, Virginia).

Paine, Rev. J. A., Jr. (New York); Palmer, Dr. E. (Arizona, Mexico, Utah); Parker, C. F. (New Jersey); Parish, S. B. (California); Parish, W. F. (California); Parry, Dr. C. C. (California, Colorado, Mexico, Minnesota, Nebraska, Utah, Wyoming); Patterson, H. N. (Illinois); Peck, C. H. (New York); Peters, Mrs. E. O. (California); Peters, T. M. (Alabama); Pierron, P. E. (Pennsylvania); Porter, T. C. (Virginia); Pringle, C. G. (New Hampshire, New Jersey, New York, Quebec, Vermont).

Reverchon, J. (Texas); Reynolds, M. C. (Florida); Robbins, Dr. J. W. (Massachusetts); Robinson, J. (Massachusetts); Rusby, H. H. (Arizona, New Jersey, New Mexico); Rust, Mrs. M. O. (New York).

Sanborn, F. G. (Kentucky); Scribner, F. L. (Maine); See, G. H. (New York); See, M. H. (New York); Shepard, E. M. (Connecticut, New Jersey, New York, Virginia); Shriver, H. (Virginia); Smith, Capt. J. D. (Florida, Maryland, North Carolina, Tennessee); Smith, Mr. (Pennsylvania); Snow, F. H. (California, Kansas); Spence, Mrs. E. J. (Ohio); Stratton, H. R. (Tennessee).

Treat, Mrs. M. (Florida); Tuckerman, E. (Massachusetts); Turner, L. M. (Alaska); Tweedy, F. (Texas).

Underwood, L. M. (New York).

Vasey, Dr. G. (Illinois).

Watt, D. A. P. (Quebec); Wheeler, C. F. (Illinois, Michigan); Whitney, G. P. (California); Wibbe, Rev. J. H. (Germany); Wilber, G. M. (New Jersey, New York, Pennsylvania); Williamson, J. (Kentucky); Wilson, J. (Kansas); Wolfe, J. (Illinois); Wright, C. (Cuba); Wright, Dr. S. H. (Delaware, New Hampshire, New York); Wright, W. G. (California).

Yates, Dr. L. G. (Vermont); Young, A. H. (Indiana); Young, H. W. (New York).

ACKNOWLEDGEMENTS

I wish to thank Miss Grace Hudson Hoysradt for supplying me with the photograph of her father and information about her father's life. I am also grateful to Dr. W. W. Payne and Dr. D. B. Ward for access to the Herbarium, University of Florida, and for reading this manuscript.

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SIXTY-SIX YEARS LATER, MICRASTERIAS FOLIACEA BAILEY AGAIN IN NEW ENGLAND

L. C. COLT, JR.

Several years ago I co-authored (Colt & Hellquist, 1971) a note which appeared in Rhodora reporting the finding of a rare species, *Micrasterias Nordstedtiana,* in Middlesex County, Massachusetts. The site of this find was Icehouse Pond, a small pond approximately one-half mile east of Route 495 on West Main Street in Hopkinton.

One does not ordinarily expect lightning to strike twice in the same place, yet among the material in a recent collection from the same station, in the same pond, and from among the same vascular aquatic, *Proserpinacea palustris* L., I have identified a number of filaments of *Micrasterias foliacea* Bailey. While it is unusual for this genus to occur in filaments, this species is readily identifiable by just this characteristic, and it is quite spectacular in appearance (Fig. 1).

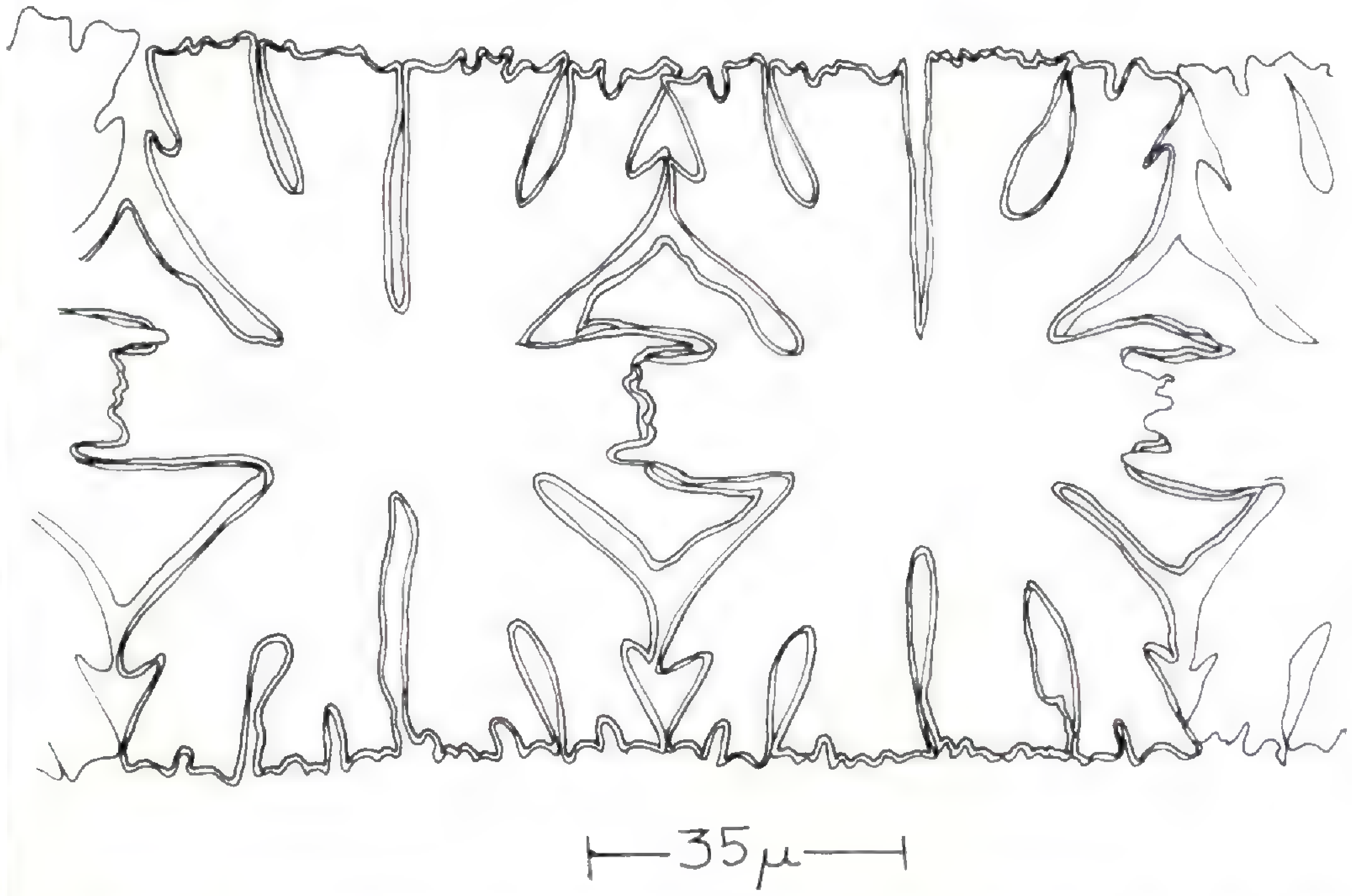

Figure 1. *Micrasterias foliacea* Bailey. From camera lucida illustration by the author.

My files show that Bailey reported the type from near Providence, R.I. (Wolle, 1882), and that Wolle collected it twice in Berkshire County, Mass. Stone (1900a) has reported it from Worcester County, and Cushman (1908b) from Carroll County, New Hampshire. It thus appears that another find has occurred in this tiny pond in Middlesex County, and as with the other species of *Micrasterias*, nearly three-quarters of a century after the previous report of its collection.

LITERATURE CITED

COLT, L. C., JR., & C. B. HELLQUIST. 1971. Seventy-five years later, a second station in New England for *Micrasterias Nordstedtiana*. Rhodora **73**: 56-57.

CUSHMAN, J. A. 1908b. New England species of *Micrasterias*. Rhodora **10**: 98-111.

STONE, G. E. 1900a. Flora of Lake Quinsigamond. Ann. Rept. Worcester Nat. Hist. Soc. 1900.

WOLLE, F. 1882. Fresh water algae VI. Bull. Torr. Bot. Club **9**: 25-30.

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EPILOBIUM PARVIFLORUM SCHREB. (ONAGRACEAE) ESTABLISHED IN NORTH AMERICA

NANCY J. PURCELL

Epilobium parviflorum Schreb., a perennial herb native to Europe and Western Asia, has been found growing wild in several counties in Ontario, Canada. Plants were first collected near Toronto in August, 1973, by the author. Seven other localities have since been discovered among misidentified specimens in several Ontario herbaria.

This species at a glance resembles a short *Epilobium hirsutum* L., but the flowers and leaves are much smaller. *Epilobium parviflorum* has the common name of "Small-flowered Hairy Willow-herb," with petals averaging only six mm. in length, while petals of *E. hirsutum* are over ten mm. long. The leaves, ranging in length from two to eight cm., vary from subsessile to sessile, but never clasp the stem, as do those of *E. hirsutum.* Both the stem and leaves have the characteristic spreading-villous pubescence of *E. hirsutum,* although the density of hairs is quite variable and tends to decrease from the base upward into a glandular puberulent inflorescence. In autumn, the plant produces short, leafy rosettes for overwintering.

Several specimens have been misidentified as *E. strictum* Muhl., which also has villous pubescence on the leaves and stems. However, *E. parviflorum* can be easily distinguished from this species by its four-lobed rather than clavate stigma, and by its oblong-lanceolate rather than linear leaves.

The discovery of this species in Ontario is noteworthy when one realizes that it has previously been reported for North America only once. Although none of the manuals for North America nor any of the North American revisions of *Epilobium* (Trelease, 1891; Munz, 1965) have included *E. parviflorum* as a member of the flora, Trelease mentioned it as having been collected on ballast at Hoboken,

New Jersey, by the Hon. Addison Brown prior to 1891. Trelease apparently considered it to be adventive from the Old World and of no importance in the flora.

Epilobium parviflorum is a species of wet streambanks, fens, and marshes. The eight localities in Ontario are quite widespread, spanning a distance of approximately one hundred miles. This makes it difficult to speculate on how the plant arrived, and how long it has actually been here. Its habitat and distribution suggest the possibility it might be native, but this cannot be verified. Because of its distinctive morphological features, it is also difficult to explain why it has been previously overlooked. It is likely to be more widespread than even the present collections indicate. Hopefully, this discovery and report of its range will alert collectors, and even further locations might soon come to light. Nevertheless, *E. parviflorum* should definitely be included as a valid element of the Ontario flora at the present time.

SPECIMENS EXAMINED:

Ontario: GREY CO.: Craigleith, clay field, Sept. 1973, *A. Campbell* s.n. (TRT 180755, TRT 180756). Rocky Saugeen, in meadow by river, 23 Sept. 1969, *G. & P. H. DuBoulay* 4622 (TRT 173238, CAN 340984). SIMCOE CO.: Wye L., Midland, in mud bordering the third beaver pond in deciduous forest, 5 Aug. 1968, *D. Haddow* 296 (DAO 114323). Vespra Tp., Conc. XIII, Lot 14, 8 mi. W. of Barrie, wet cedar-tamarack swamp, 8 Aug. 1973, *L. Nyman* 3478 (Herbarium of A. A. Reznicek and R. S. W. Bobbette). Tiny Tp., Conc. XX, Lot 1, moist open edge of stream, 30 July 1969, *A. A. Reznicek* 948 (Herbarium of A. A. Reznicek and R. S. W. Bobbette). Flos Tp., Conc. IX, lot 25, Ontario Zoological Park, Wasaga Beach, moist ground along beaver pond in trough between wooded low dune ridges, 29 July 1973, *R. S. W. Bobbette* 3701 (TRT 180757). YORK CO.: Toronto Island, wildlife area — yard sector, 10 Aug. 1973, *V. Popov* 238 (Herbarium of Metropolitan Toronto Parks Department 976). Morningside Park, Toronto, 43°46′, 79°10′, wet streambank, 14 Aug. 1973, *N. Purcell* and *B. Wyatt* s.n. (TRT 180752, TRT 180753).

I would like to acknowledge the loan of specimens from the cited herbaria, and thank Dr. J. W. Grear for his helpful criticism of the manuscript.

LITERATURE CITED

MUNZ, P. A. 1965. Onagraceae, in North American Flora **2**(5): 198-225. New York Botanical Garden, New York.

TRELEASE, W. 1891. A Revision of the American Species of *Epilobium* Occurring North of Mexico. Report of the Missouri Bot. Gard. **2**: 67-117, 48 plates.

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CANADA

SCOTCH PINE AS AN ASSOCIATE OF THE TESSELATED RATTLESNAKE PLANTAIN: The Tesselated Rattlesnake Plantain (*Goodyera tesselata* Lodd.) grows at only a few stations in Rhode Island, but recent observations have convinced me that it has a partiality for the duff of Scotch Pine (*Pinus sylvestris* L.).

In August 1972, acting on a tip from Lewis Carpenter of Hope, R.I., I visited Carolina State Forest in Washington County, where the year before, Carpenter had found countless hundreds of the orchid plants growing under Scotch Pine. Unfortunately, by the time I visited, the main grove had been clear-cut, leaving not one tree standing and not one orchid. Nevertheless, marginal stands of Scotch Pine did have the *Goodyera* in abundance. The landscape is rolling at this site, and the *Goodyera* does not grow on the droughty knolls even though they are clad with Scotch Pine, but rather on the cooler slopes, and especially on the flats under the introduced pine. There it abounds. The plants grow strictly under that pine, not under *Pinus strobus*, *Pinus resinosa* or *Pinus rigida*, which also occur interspersed at the location. *Goodyera tesselata* grows only under the immediate spread of Scotch Pine.

Goodyera pubescens Willd., on the other hand, which outnumbers *G. tesselata* ten thousand to one in this state, grows not under the Scotch Pine, but under mixed white pine and oak cover.

This clear-cut preference of the orchid set me to searching other stands of Scotch Pine for an orchid I had hitherto considered very scarce. At the two or three stations where I have seen it in its natural habitat, that is, under White Pine or in one case under Hemlock, it hardly numbers fifteen or twenty plants. Rhode Island is nearly the southern boundary of its range.

At two stations of Scotch Pine, one at Woody Hill Management Area, Washington County, and a small one-quarter acre stand in West Greenwich, Kent County, the orchid is absent. I would account for its absence by the

dry, upland conditions and the young stage of the pines there. However, at Foster, Providence County, under an acre of Scotch Pine known to have been set out before World War I, the orchid occurs in great quantity, perhaps two hundred on flat terrain where the water table is rather high. Scotch Pine here mingles with White Spruce (*Picea glauca* Moench), but the *Goodyera* shuns the spruce. It grows only under the spread of Scotch Pine.

The Scituate Reservoir Watershed in Providence County provides a good test for this observation, as it has multi-acre tracts of conifers, most of them plantations, with Red Pine, White Pine and White Spruce most abundant. On this watershed I investigated four Scotch Pine sites in company with the watershed manager, Hans Bergey, a professional forester. At the first stand, a mere handful of Scotch Pines mixed with other pines on a steep slope where competition was strong from bayberry and other bushes, the orchid did not appear. By contrast, at Clayville and at two North Scituate stands *Goodyera* flourishes, blooming the third week in July. Here, it was noted, the fallen Scotch Pine needles formed a mulch of about three inches depth above mineral soil. The trees had been set out in 1934-35, and the largest of them had diameters up to fifteen inches. At all three sites *Goodyera tesselata* showed the familiar partiality to the Scotch Pine, entirely shunning the other conifers.

If any conclusion can be drawn from these observations, it is that an introduced tree has encouraged the spread of a native species of orchid. It might prove worthwhile for students of botany to search other groves of Scotch Pine for the occurrence of the Tesselated Rattlesnake Plantain. Perhaps the tree has extended this orchid beyond its normal, northerly range.

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ISOPYRUM BITERNATUM (RAF.) T. & G. (RANUNCULACEAE) NEW TO VIRGINIA AND ITS DISTRIBUTION EAST OF THE APPALACHIAN MOUNTAINS: While making collections along the Hyco River in Halifax County, Virginia, for the University of North Carolina Herbarium at Chapel Hill, we discovered a large population of *Isopyrum biternatum* (Raf.) T. & G. The infrequency of this plant east of the Appalachian Mountains led us to make a herbarium and literature search. No reports or specimens from Virginia were found, indicating that the Hyco River site is the first station for this species in the state.

This population of *Isopyrum* grows in the flat bottoms of the alluvial woods behind natural levees. Other interesting or relatively uncommon plants associated with it here at the Virginia site are *Viola eriocarpa* Schweinitz var. *eriocarpa, Cardamine douglasii* (Torrey) Britton, *Anemonella thalictroides* (L.) Spach, *Carex jamesii* Schweinitz and *Ranunculus micranthus* Nuttall ex T. & G. The levees are covered with *Mertensia virginica* (L.) Persoon which forms nearly unbroken bands of color along both sides of the river when *Isopyrum* is in flower.

Isopyrum was unknown east of the Appalachian Mountains until 1950 when it was found along the Eno River in Durham County, North Carolina, by Blomquist (Fox *et al.,* 1950). Since then additional stations have been found in other counties in the Carolinas: North Carolina, Lee Co. (Radford, 1952); Harnett Co. (Radford *et al.,* 1968); South Carolina, McCormick Co. (Radford, 1959). To this list can be added Person County, North Carolina, where we collected *Isopyrum* along the Hyco River south of the Virginia line on 29 March, 1974 (*Boufford* 12561 & *Massey,* NCU).

It seems unlikely that *Isopyrum biternatum* is a recent addition to the flora of the Piedmont, but it probably has been overlooked due to its early flowering time, its resemblance to the more widespread *Anemonella thalictroides,* and the often unappealing appearance of the habitat in

which it grows. It seems highly probable that searches along other major streams on the outer edge of the Piedmont will produce other stations for this species.

Specific collection data for the Virginia specimen are as follows: HALIFAX CO.: floodplain of Hyco River, junction of US Highway 501 and Hyco River, south of South Boston; flowers white, perennial, very abundant, growing with *Mertensia;* 12 April, 1974, *Massey* 3867 & *Boufford.*

We wish to thank the curators of the following herbaria for providing specimens and other assistance: G, WILLI, LYN, FARM, VCU, VPI.

LITERATURE CITED

FOX, WILLIAM B., R. K. GODFREY, & H. L. BLOMQUIST. 1950. Notes on distribution of North Carolina plants. Rhodora **52**: 253-271.

RADFORD, A. E. 1952. Range extensions in the flora of North Carolina. J. Elisha Mitchell Sci. Soc. **68**: 105-108.

————. 1959. A relict plant community in South Carolina. J. Elisha Mitchell Sci. Soc. **75**: 33-34.

————., H. E. AHLES, & C. R. BELL. 1968. Manual of the Vascular Flora of the Carolinas. University of North Carolina Press, Chapel Hill.

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EDITOR'S NOTE: DATE OF ISSUE OF JANUARY NUMBER.

The date of issue of the January, 1976, number of Rhodora, being Vol. 78, No. 813, including pages 1-168, was April 30, 1976.

EDITORIAL ANNOUNCEMENT: CHANGE OF EDITORSHIP.

With the completion of the current volume (78) of Rhodora in December my term of service as Editor-in-Chief will, of necessity, come to an end. I would like to take this opportunity to thank the Associate Editors and the many friends and colleagues who, voluntarily and anonymously, contributed their time and effort to the reviewing of manuscripts. Their contributions have constituted a major contribution to the journal, and are deeply appreciated.

As of January 1, 1977, Dr. Rolla M. Tryon, Gray Herbarium, Harvard University, will be the new Editor-in-Chief.

Contributors are advised to continue sending all manuscripts, and correspondence relating to manuscripts, to Ms. H. Spongberg, Managing Editor, Rhodora, Harvard University Herbaria Bldg., 22 Divinity Ave., Cambridge, Mass. 02138.

Rhodora

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